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Polarized growth and cell studies on the Avena coleoptile, phytohormone test object

GEORGE S. AVERY, JR. AND PAUL R. BURKHOLDER

(WITH SIX FIGURES)

INTRODUCTION

Our knowledge of plant hormone activity has grown up chiefly through studies made upon the growth and tropisms of the *Avena* coleoptile. Experiments in which known amounts of growth hormone (contained in agar blocks) were placed upon decapitated coleoptiles, have shown that within certain limits, growth intensity is proportional to the concentration of the hormone, (Went, 1928; Thimann and Bonner, 1933). It would appear, therefore, that its natural distribution in plants is causally associated with growth patterns of developing organs. This has been demonstrated in a preliminary way in *Avena* coleoptiles (Thimann, 1934) and in *Nicotiana* leaves (Avery, 1935), where zones of more rapid increase in length have been shown to possess greater amounts of the hormone.

The gross morphological structure and development of the *Avena* coleoptile (standard test object in the quantitative determination of plant hormones) are moderately well understood, but comparatively little attention has been given to the cell and tissue changes involved in its growth and development. Since no mitoses were found in prepared sections of the growing coleoptile (Tetley and Priestley, 1927), observers have concluded that this second leaf of the oats seedling grows almost entirely by the enlargement of cells already present (laid down during embryogeny). Observations made on the number of cells in the epidermis of the growing coleoptile (*Zea* and *Avena*) showed that these cells actually do not multiply (Tetley and Priestley, 1927), although the over-all length of the coleoptile may increase many fold. This information, together with other data, led to the generally accepted conclusion that growth hormones are involved solely in cell elongation.

The fact that cell division was found in the rapidly elongating basal portion of the *Nicotiana* leaf where the auxin concentration was high, suggested a possible rôle of the hormone in cell division (Avery, 1935). Furthermore, pure "heteroauxin" has been demonstrated to promote cell division in the cambium (Snow and LeFanu, 1935), and in callus tissue (Laibach, Mai, and Müller, 1934). In the light of these discoveries it seemed possible that cell division, as well as cell elongation, might be contributing to growth of the *Avena* coleoptile.

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MATERIALS AND METHODS

Avena sativa seeds of the pure line "Siegeshafer" were obtained from Dr. E. Å. Åkerman of Svalöv, Sweden. The wheat used was *Triticum vulgare* var. Marquis, supplied by the U. S. Department of Agriculture,

TABLE 1

Avena. *Segment size and ratio of segment growth to that of the coleoptile as a whole in successive stages of its development.*

STAGES (SEGMENT LENGTHS IN MM.)		I		II		III		IV		V
GROWTH RATIOS IN STAGE INTERVALS			I–II		II–III		III–IV		IV–V	
	Series									
a segment	1	1	.57	1.69	.68	1.93	.75	2.08	.88	2.34
	2	1	.73	1.85	.68	2.16	.76	2.52	.88	3.20
	3	1	.62	1.69	.53	2.02	.93	2.66	.85	2.71
	4	1	.63	1.45	.51	1.83	.93	2.70	.96	2.95
b segment	1	1	1.00	2.98	.89	4.70	.91	6.56	1.18	8.72
	2	1	1.10	2.80	.97	4.68	1.00	7.20	1.10	11.40
	3	1	.97	2.66	.95	5.72	1.06	8.57	1.06	10.88
	4	1	.98	2.24	.93	5.22	1.10	9.09	1.14	11.81
c segment	1	1	1.11	3.31	1.06	5.87	1.08	9.20	1.06	12.49
	2	1	1.16	2.95	1.16	5.89	1.08	9.79	1.22	13.70
	3	1	1.10	3.00	1.14	7.78	1.02	11.20	1.08	14.50
	4	1	1.14	2.61	1.13	7.37	1.09	12.70	1.02	14.79
d segment	1	1	1.29	3.93	1.13	7.41	1.02	10.96	.94	13.12
	2	1	1.00	2.57	1.08	4.80	1.00	7.36	.98	10.40
	3	1	1.34	3.58	1.15	9.35	.97	12.82	.91	14.00
	4	1	1.26	2.89	1.18	8.54	.88	11.90	.88	12.06

Number of plants and average over-all length of coleoptiles in the four experimental series given above.

SERIES	NUMBER OF PLANTS	DEVELOPMENTAL STAGES				
		I	II	III	IV	V
1	32	4	11.91	19.91	28.80	36.67
2	18	4	10.17	17.53	26.87	38.70
3	20	4	10.93	24.87	35.25	42.09
4	16	4	9.19	22.96	36.39	41.61

Washington, D. C. Seeds were soaked in tap water for several hours and then were placed upon moist filter paper in glass germinating dishes and kept in diffuse light in the laboratory for one day. Further germination and growth took place in a dark room, lighted for intermittent observations only with phototropically inactive ruby glass Mazda lamps. During

the early period of germination the seedlings adhering to the moist filter paper were kept in a nearly vertical position in order to avoid growth curvatures which might have taken place due to geotropic stimulation. When the coleoptiles attained a length of 4 mm., those that were uniform were placed in specially constructed glass holders which permitted erect growth of the coleoptile. The plants were grown in tap water. A fine camel's hair brush and powdered carbon black suspended in lanolin were used for marking the coleoptiles into segments, under a binocular microscope. Subsequent growth took place in a moist thermostatic chamber where the relative humidity was about 90% and the temperature was approximately 26°C.

TABLE 2

Triticum. *Segment size and ratio of segment growth to that of the coleoptile as a whole in successive stages of its development. The data represent averages of a total of 17 plants.*

STAGES (SEGMENT LENGTHS IN MM.)	I		II		III		IV		V
GROWTH RATIOS IN STAGE INTERVALS		I–II		II–III		III–IV		IV–V	
a segment	1	.69	1.69	.76	2.32	.70	2.98	.96	3.94
b segment	1	.96	2.35	.98	4.19	.91	7.02	1.14	11.22
c segment	1	1.05	2.57	1.07	4.98	1.08	9.93	1.11	15.44
d segment	1	1.31	3.22	1.09	6.37	1.11	13.07	.86	15.84
Average overall coleoptile length in millimeters	4		9.83		17.86		33.00		46.44

Details of the experiments follow, but it should be mentioned here that one inherent difficulty lay in estimating the exact position of the basal end of the coleoptile. Some of the plants which were marked later gave clear indication of inaccurate marking, the lanolin having been applied either just above or below the coleoptilar node. Only those coleoptiles which grew straight and gave evidence of having been marked correctly at the 4 mm. stage were kept for later observations. Subsequent measurements were made to tenths of a millimeter under a binocular microscope. The experiments on *Avena* were repeated four times. Series I was made up of 32 plants; series II, 18 plants; series III, 20 plants; and series IV, 16 plants (table 1). In a similar study of *Triticum* 17 uniform plants were carried through from germination to maturity of the coleoptiles (table 2).

At different stages of growth from the embryo to maturity, a certain number of representative coleoptiles were selected, cut into segments and

preserved for microscopic study. In preliminary trials with formol-acetic-alcohol, Carnoy's and Nawaschin's fluids, the best results were obtained in the last named fixing solution. The usual steps were followed in dehydration and paraffin infiltration, and longitudinal sections were cut at thicknesses ranging from 10 to 24 microns. Crystal violet was used for staining.

Examinations of the slides gave indication of differential shrinkage of the segments, and further observations showed that most of this shrinkage took place during dehydration and paraffin infiltration. The tip of the coleoptile (segment *a*, fig. 1) was subject to almost no shrinkage, whereas

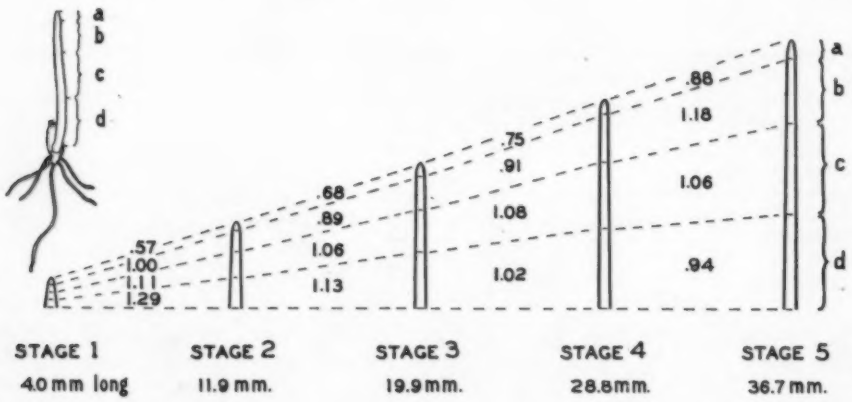

Fig. 1. Diagrams of the *Avena* coleoptile at different stages of development. Coleoptiles 4 mm. long (stage I) were marked into four 1 mm. segments (*a*, *b*, *c*, *d*), and the length of each was measured in several later stages of growth. The figures between stages indicate the ratio of the increase in segment length to increase in the length of the coleoptile as a whole (see text). Most of the increase in coleoptile length is due to greater relative elongation of segments *b*, *c*, and *d*. Note that the growth of segment *a* relative to the coleoptile as a whole increases as the coleoptile grows older, while the relative growth rate of segment *d* decreases with age. Data from table 1, series 1.

in segments *c* and *d*, shrinkage was often as much as 10%. Due to the differential shrinkage in length of the prepared sections, in contrast with the living tissues, it was not possible to determine cell lengths without making necessary corrections for this shrinkage.

The number and size of the cells in each segment were obtained for all the stages in coleoptile growth. Due to the extreme elongation of the epidermal cells and the consequent difficulties of obtaining full length median sections, it was necessary to use living material for observations on this layer.

The embryonic coleoptiles (fig. 3) were not marked and cut into seg-

ments before sectioning. Their over-all length was divided into four equal parts, corresponding to segments *a*, *b*, *c*, and *d* of the later stages. The cells were measured and counted in each layer (epidermis, subepidermis, etc.) of each segment. From these data it was possible to ascertain to what extent cell multiplication and cell elongation participated in the growth of the coleoptile.

DIFFERENTIAL GROWTH RATES

In order to determine relative growth rates in different portions, growing coleoptiles 4 mm. in length were marked off into four 1 mm. segments, and the length of each was measured in several later stages of development. The *ratio* of the increase in segment length to increase in the length of the coleoptile as a whole, i.e., "k," was then determined for each growth period as follows:

$$\text{"k"} = \frac{\dfrac{\text{segment length stage}_2}{\text{segment length stage}_1}}{\dfrac{\text{coleoptile length stage}_2}{\text{coleoptile length stage}_1}}$$

$$\text{or, "k"} = \frac{\text{segment growth}}{\text{coleoptile growth}}$$

Example: The mean length of segment *a*, stage IV, is 2.08 mm., and this increases to 2.34 mm. in stage V. Meanwhile the average length of the coleoptile increases from 28.80 mm. to 36.67 mm. The growth of the segment may be expressed as follows:

$$\frac{\text{segment } a_{\text{V}}\ 2.34}{\text{segment } a_{\text{IV}}\ 2.08} = 1.125,$$

and the increase of the whole coleoptile may be stated as:

$$\frac{\text{coleoptile}_{\text{V}}\ 36.67}{\text{coleoptile}_{\text{IV}}\ 28.80} = 1.274$$

Then, $\dfrac{\text{segment growth of } 1.125}{\text{coleoptile growth of } 1.274} = 0.884 = \text{"k,"}$ or, the segment growth rate = .884 × coleoptile growth rate.

Such calculations yield simple quantitative expressions of differences in the growth rate of various segments of the coleoptile relative to its growth as a whole, at different periods of its development. If "k" for a particular segment between any two stages = 1, it indicates that the segment is increasing in length at the same rate as the coleoptile as a whole; if less than 1, that the segment is growing at a slower rate than the structure

as a whole, or, if greater than 1, proportionally greater than the coleoptile as a whole.

Figure 1 shows five stages in the development of the coleoptile. Segment *a* is growing relatively more rapidly as the coleoptile matures (0.57, 0.68, 0.75, 0.88). In the last stage of coleoptile elongation, segment *a* is growing about 88/100 as rapidly as the organ as a whole. The figures for intermediate stages of the elongation of segment *b* do not show successive increases, but it is clear that the segment is growing more rapidly toward the end of its development than in the beginning; segments *a* and *b* are similar therefore in speeding up their relative growth rate as the coleoptile nears maturity. Segment *c* elongates at a rate about equal to that of the coleoptile as a whole, and maintains this rate throughout development. Segment *d*, in contrast to the behavior of the upper segments, grows relatively more slowly as the coleoptile elongates. The decrease in relative growth rate of this segment is compensated for by the acceleration of segments *a* and *b*.

The shift in position of the zone of maximum growth rate is more graphically shown in figure 2. As the coleoptile approaches maturity, growth slows down throughout its length, ceases at its base, and becomes relatively greater near its apex. After the leaf bursts through, growth is even more sharply localized in the tip segment.

CELL NUMBER AND SIZE

The number and size of the cells in the epidermis, subepidermis, third layer, fourth layer and the inner epidermis were determined in median longitudinal sections for each of four segments at six stages in the growth of the coleoptiles of *Avena* and *Triticum*. The vascular tissues were not included in this study. Determinations of average cell number in each layer in the *Avena* coleoptiles are presented in table 3 and in figure 5. Similar data for *Triticum* are given in table 4. The number of epidermal cells in the coleoptile remains constant from the embryo to maturity. It is about thirty cells from tip to base in the embryonic condition, and

Fig. 2. *Avena* coleoptile. Diagrams to show shift in position of the zone of maximum growth intensity. Coleoptiles were marked as indicated at the left, and in the upper four experiments were allowed to grow until the time when the foliage leaf ordinarily bursts through. The individual segments were then measured and the percentage increase in length was determined for each. The latter is indicated in the right hand column. The density of the dots as well as the percentage figures indicate growth intensity and the shift in the region of maximum growth from the base in the young coleoptile to the apical region in maturing coleoptiles. Growth is slowing down throughout while this change is taking place. Each diagram represents data from a single coleoptile selected as typical from a group of at least three similarly marked.

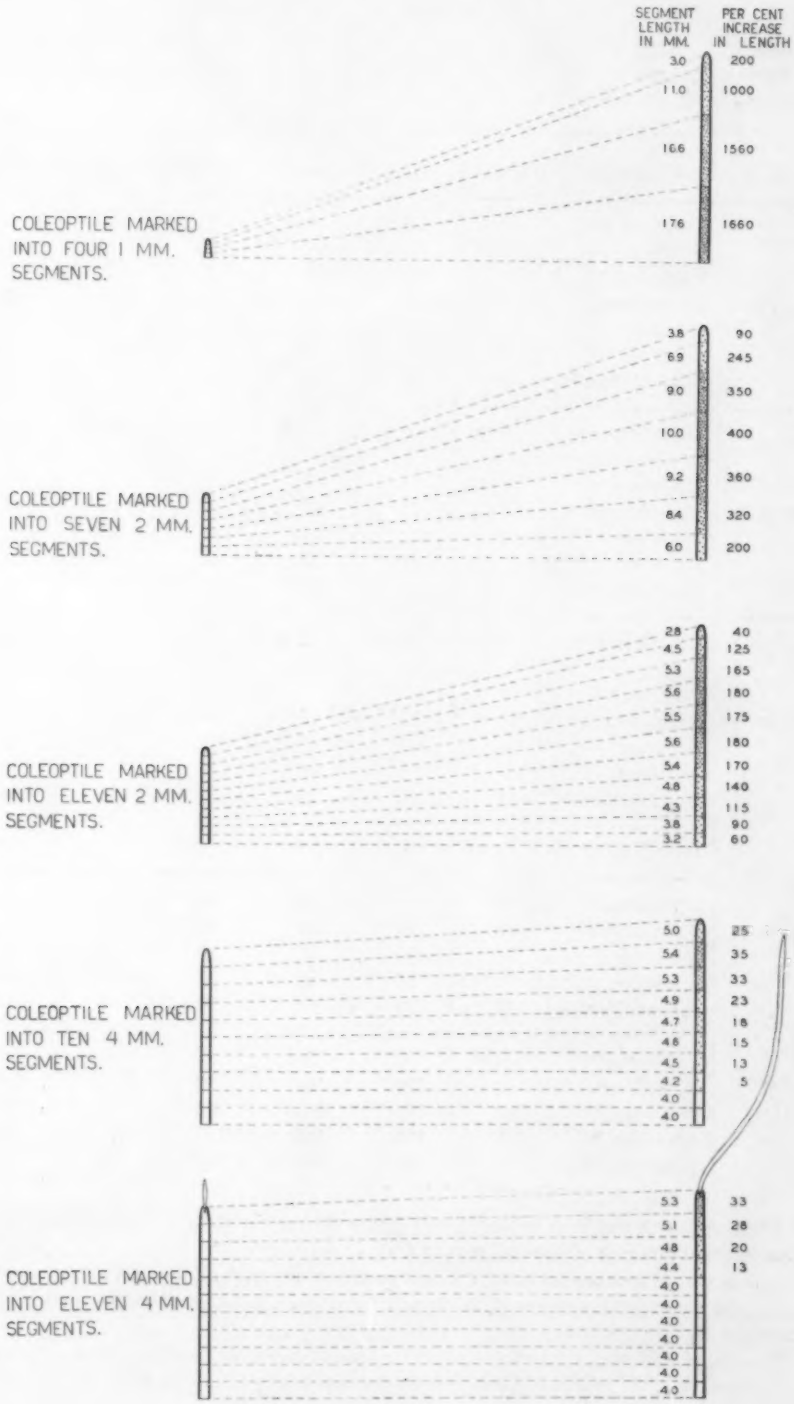
SEGMENT LENGTH IN MM.
PER CENT INCREASE IN LENGTH
COLEOPTILE MARKED INTO FOUR 1 MM. SEGMENTS.
3.0 200
1.10 1000
1.66 1560
1.76 1660
COLEOPTILE MARKED INTO SEVEN 2 MM. SEGMENTS.
3.8 90
6.9 245
9.0 350
10.0 400
9.2 360
8.4 320
6.0 200
COLEOPTILE MARKED INTO ELEVEN 2 MM. SEGMENTS.
2.8 40
4.5 125
5.3 165
5.6 180
5.5 175
5.6 180
5.4 170
4.8 140
4.3 115
3.8 90
3.2 60
COLEOPTILE MARKED INTO TEN 4 MM. SEGMENTS.
5.0 25
5.4 35
5.3 33
4.9 23
4.7 18
4.6 15
4.5 13
4.2 5
4.0
4.0
COLEOPTILE MARKED INTO ELEVEN 4 MM. SEGMENTS.
5.3 33
5.1 28
4.8 20
4.4 13
4.0
4.0
4.0
4.0
4.0
4.0
4.0

TABLE 3

Avena. *Cell number in different portions (tip to base) of the coleoptile in successive stages of its development. Stages I, II, III, IV and V represent averages of 3 to 5 coleoptiles each, stage VI, 13 coleoptiles.*

STAGES (OVER-ALL LENGTH OF COLEOPTILES)		I[1] (1.62 MM.)	II (4 MM.)	III (9.83 MM.)	IV (17.86 MM.)	V (33 MM.)	VI (46.44 MM.)
	Length in mm.	0.41	0.9	1.8	1.9	2.6	2.5
a segment[2]	Epidermis	7	8	9	7	7	7
	Subepidermis	12	26	34	29	32	30
	3rd layer	11	25	33	29	33	29
	4th layer		25	32	27	26	27
	Inner epidermis	8	19	20	20	19	22
	Length in mm.	0.41	0.9	2.4	5.2	8.2	11.2
b segment	Epidermis	7	6	7	5	6	7
	Subepidermis	15	34	47	62	55	57
	3rd layer	16	31	41	51	46	51
	4th layer		28	35	46	43	43
	Inner epidermis	12	21	25	33	33	30
	Length in mm.	0.41	0.9	2.9	7.1	10.7	13.1
c segment	Epidermis	8	6	7	5	7	6
	Subepidermis	16	37	55	57	57	58
	3rd layer	18	32	47	52	50	52
	4th layer		28	41	46	41	46
	Inner epidermis	15	26	33	39	42	40
	Length in mm.	0.41	0.9	3.2	6.2	11.4	12.6
d segment	Epidermis	11	9	8	6	8	6
	Subepidermis	17	32	48	44	47	50
	3rd layer	16	30	42	44	43	44
	4th layer		27	40	38	41	38
	Inner epidermis	16	29	41	36	35	37
Totals	Epidermis[3]	33	29	31	23	28	26
	Subepidermis	60	129	184	192	191	195
	3rd layer	61	118	163	176	172	176
	4th layer		108	148	157	151	154
	Inner epidermis	51	95	119	128	129	129

[1] Embryos which had been soaked for 24 hrs. were used in stage I. Actual length of the *dormant* embryos (average of 5) = 0.67 mm.

[2] 1/10 of tip not counted because, *first*, that portion of the segment does not elongate as does the balance of the segment, and *second*, all the active cell layers in which cell counts were made do not continue on into the tip.

[3] The actual epidermal cell counts from tip to base of coleoptile including the 1/10 excluded above in segment *a*, are as follows for the six stages respectively: 34, 32.4, 35.2, 28.5, 32.5, 31.2.

TABLE 4

Triticum. *Cell number in different portions (tip to base) of the coleoptile in successive stages of its development. Data taken from an average of 2 to 5 coleoptiles for each stage.*

STAGES (OVER-ALL LENGTH OF COLEOPTILES)		I[1] (0.76 MM.)	II (3.9 MM.)	III (10.2 MM.)	IV (17.79 MM.)	V (32.61 MM.)	VI (40.35 MM.)
a segment[2]	Length in mm.	0.19	0.90	1.58	1.88	2.48	3.60
	Epidermis	7	12	8	10	8	13
	Subepidermis	8	22	22	21	17	23
	3rd layer	9	18	21	21	21	20
	4th layer		22	21	20	21	24
	Inner epidermis	8	11	12	13	12	13
b segment	Length in mm.	0.19	1.00	2.38	4.33	7.13	10.75
	Epidermis	9	8	8	10	9	8
	Subepidermis	11	32	39	41	47	54
	3rd layer	12	23	33	37	38	41
	4th layer		24	35	36	38	40
	Inner epidermis	12	11	13	17	18	20
c segment	Length in mm.	0.19	1.00	2.75	5.08	11.00	11.00
	Epidermis	11	10	10	13	14	8
	Subepidermis	12	36	57	56	65	74
	3rd layer	12	34	48	48	58	57
	4th layer		33	48	49	51	63
	Inner epidermis	13	16	18	20	25	27
d segment	Length in mm.	0.19	1.00	3.50	6.50	12.00	15.00
	Epidermis	14	12	16	12	13	15
	Subepidermis	11	33	51	48	57	67
	3rd layer	12	26	53	49	50	61
	4th layer		26	54	47	48	61
	Inner epidermis	13	20	29	29	29	29
Totals	Epidermis[3]	41	42	42	45	43	44
	Subepidermis	42	123	169	166	186	218
	3rd layer	45	101	155	155	167	179
	4th layer		105	158	152	158	188
	Inner epidermis	46	58	72	79	84	89

[1] The embryo (dry) was used as stage I.

[2] 1/10 of tip not counted because, *first*, that portion of the segment does not elongate as does the balance of the segment, and *second*, all the active cell layers in which cell counts were made do not continue on into the tip.

[3] The actual epidermal cell counts from tip to base of coleoptile including the 1/10 excluded above in segment *a*, are as follows for the six stages respectively: 42, 48, 44, 46, 47, 44.

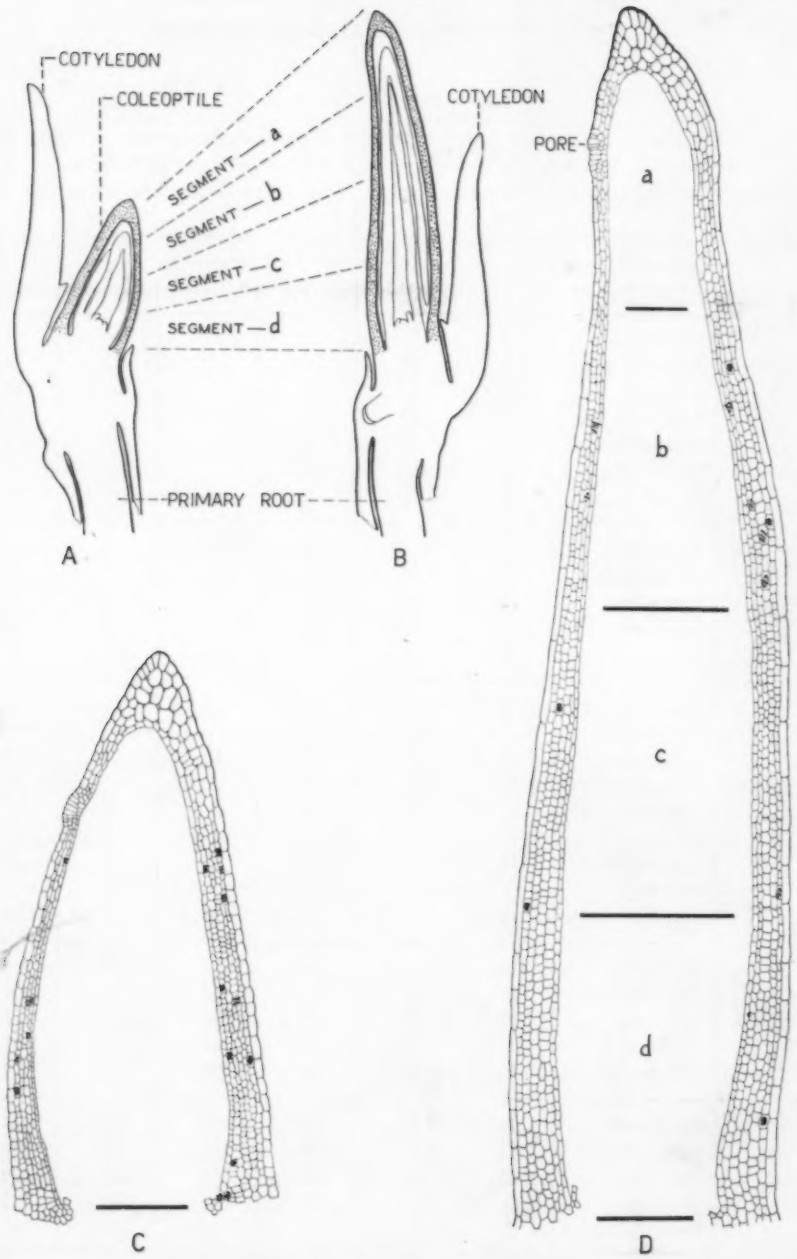

Fig. 3. A and B, diagrams of median longitudinal sections through germinating embryos of *Avena* at two different ages, ×40. In these two stages (I and II, table 3) of development, the coleoptile was divided into 4 segments of equal length. C and D, detailed drawings of the coleoptiles of the above embryos (1.62 and 4 mm. long, respectively), with segments indicated by heavy lines. Mitoses are evident throughout. Cell number determinations (stages I and II, table 3) in the epidermis, subepidermis, third layer, fourth layer and inner epidermis of the different segments were made from such sections.

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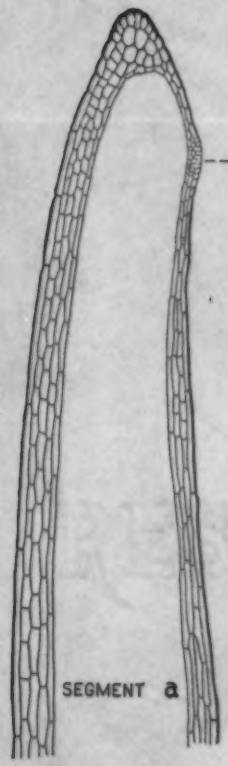
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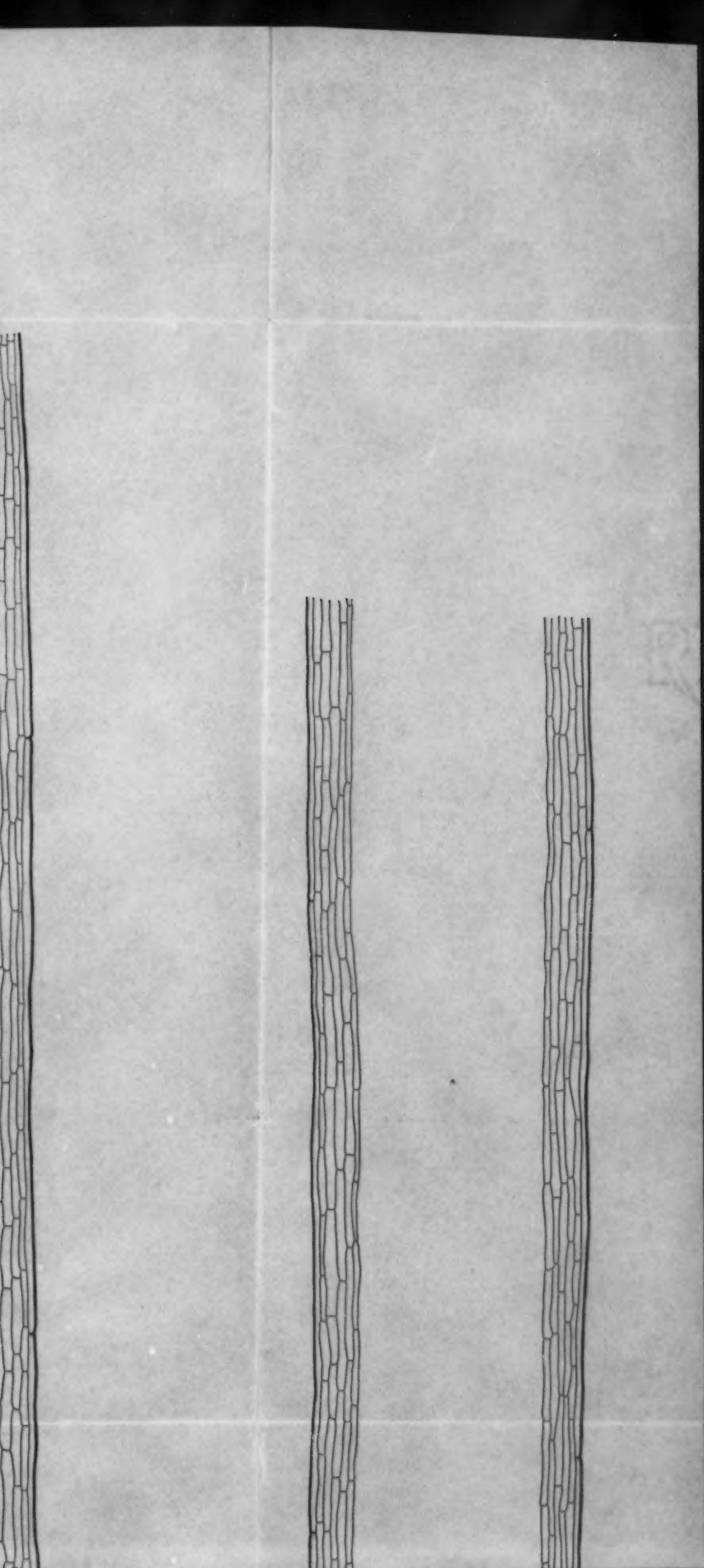
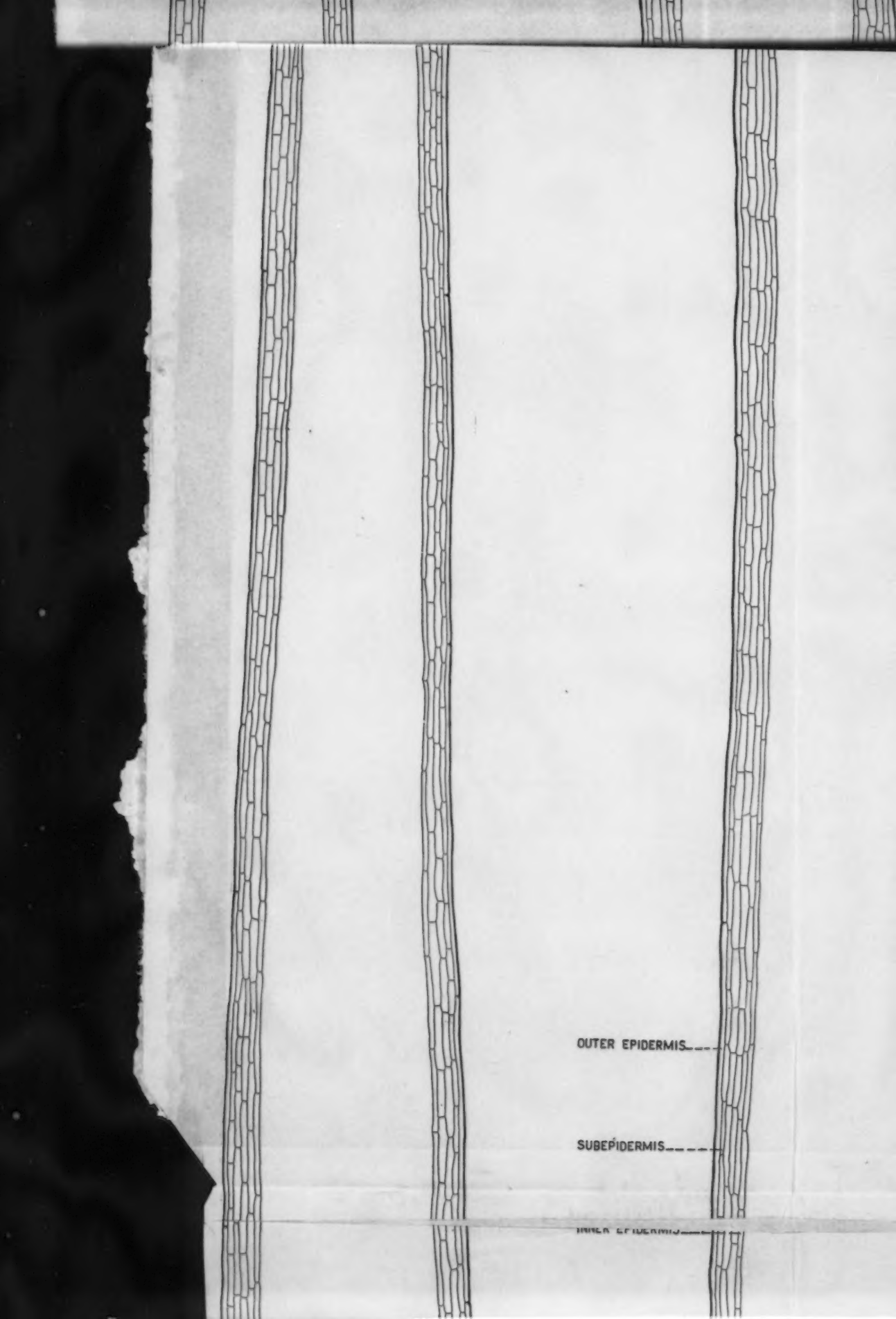
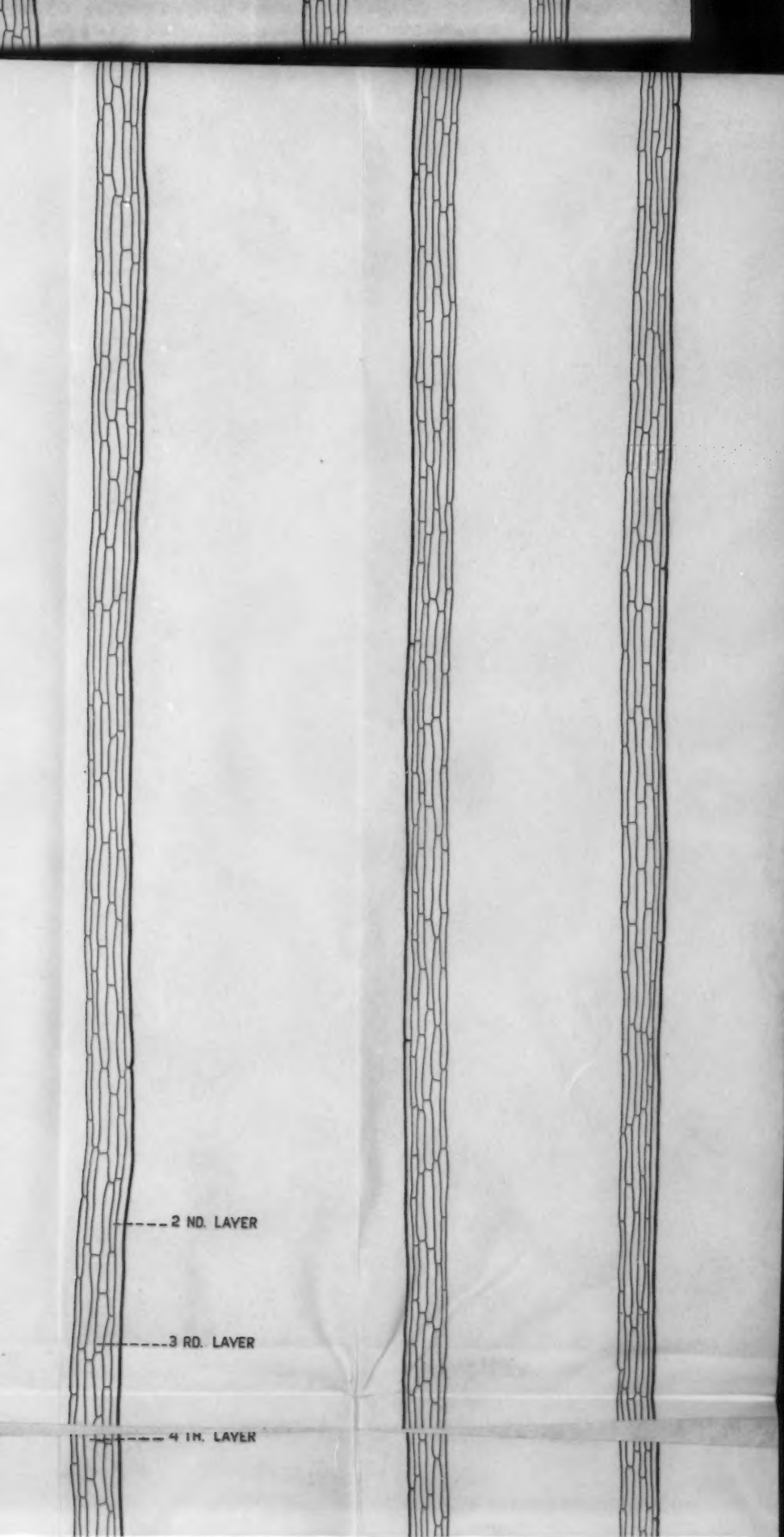



OUTER EPIDERMIS
SUBEPIDERMIS


2 ND. LAYER
3 RD. LAYER
4 TH. LAYER

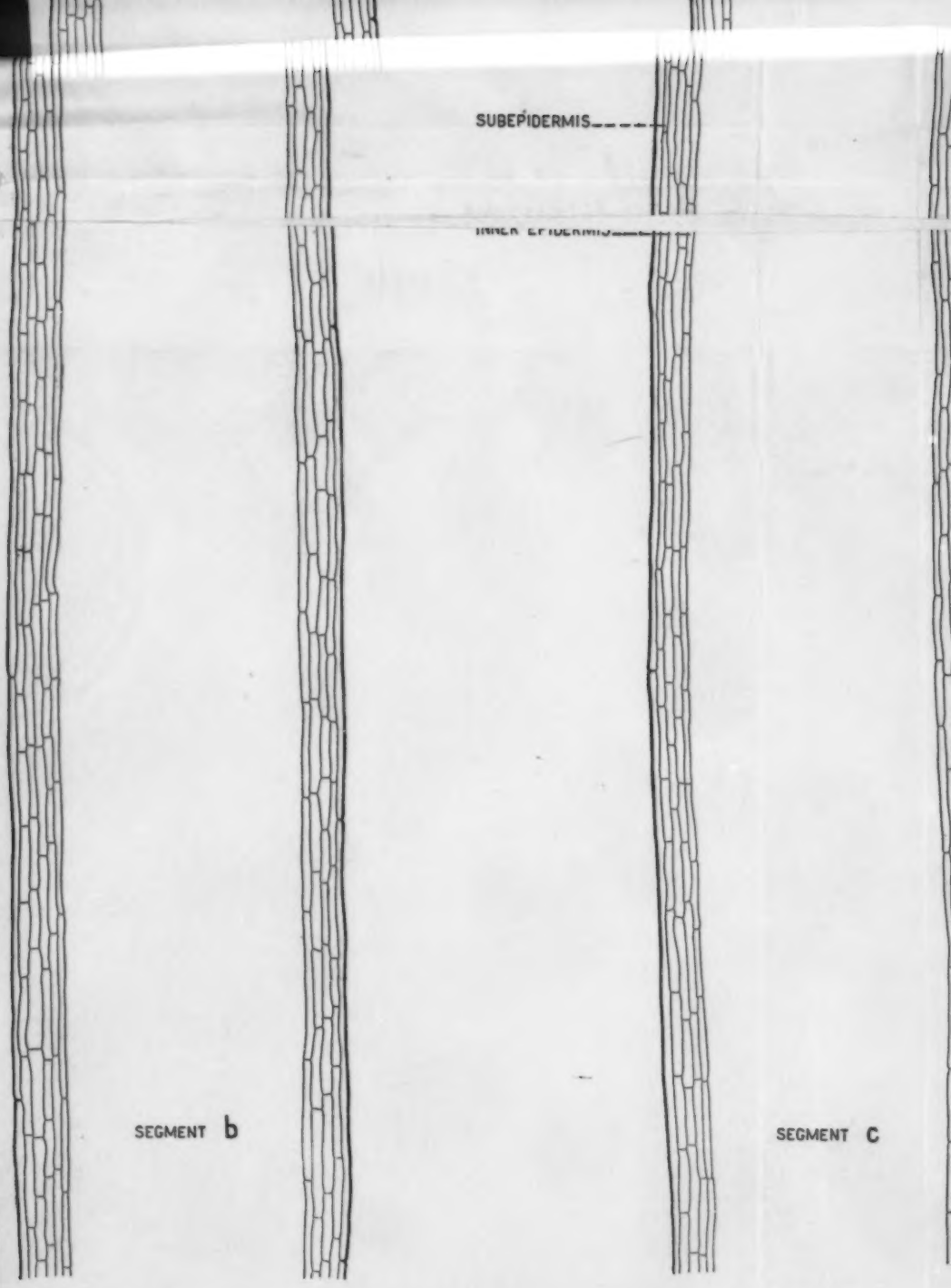
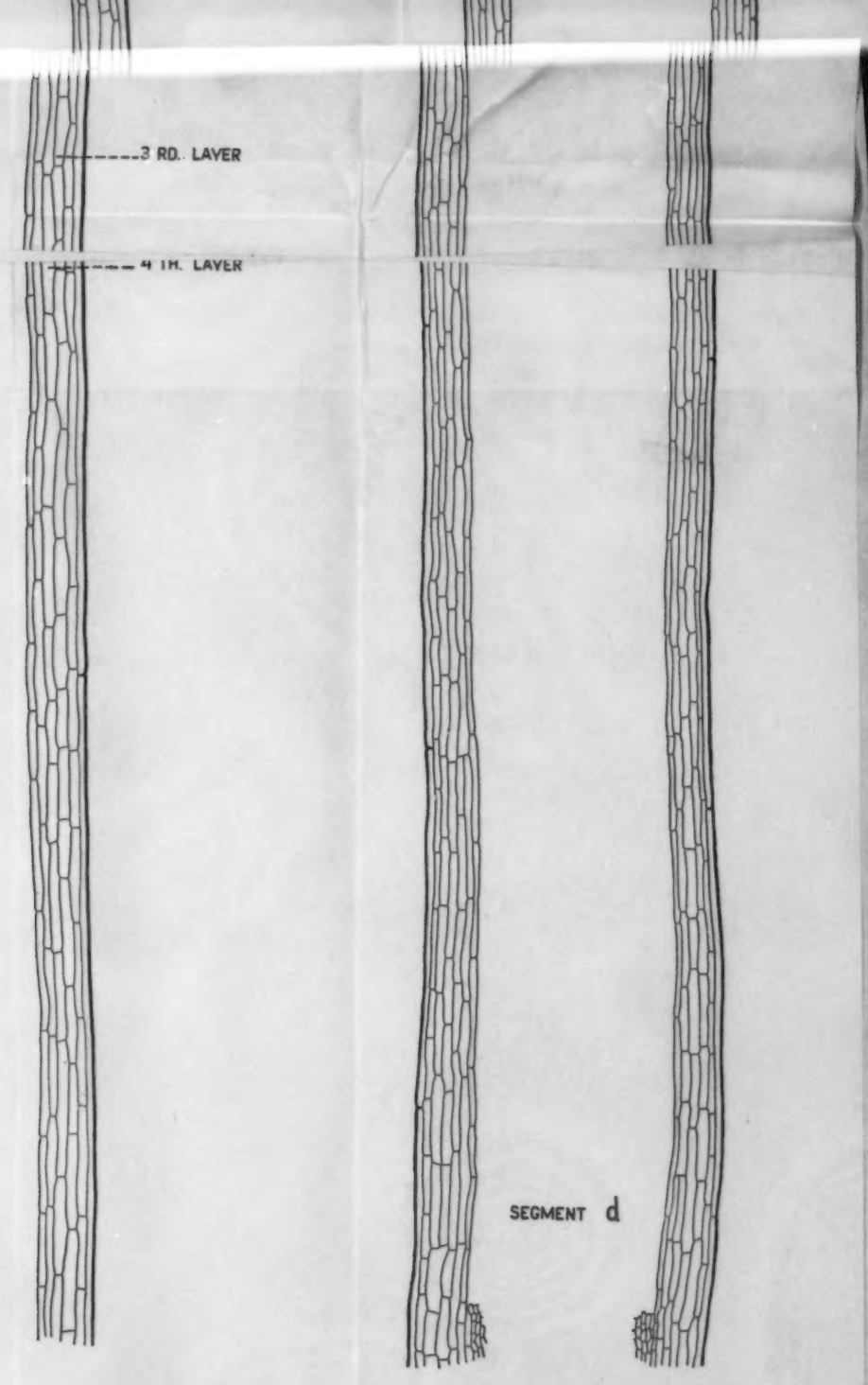


Fig. 4. Drawings (made with the aid of a microprojector) of median longitudinal sections throug
segments were of equal length (1 mm.) when the young coleoptile was only 4 mm. long. Due to differe
example, segment *a* grew relatively little compared with the other three segments. The tip portion of
pare fig. 3, C and D). For the number of cells in the different layers, see table 3, stage VI. For the inc
figure 5.



rough segments *a*, *b*, *c*, and *d* of the mature *Avena* coleoptile, ×40. All these
fferential growth rates, the various segments attain different lengths; foe
n of segment *a* (above the "pore" region) shows no increase in length (com-
e increase in cell number in the different layers from embryo to maturity, ser

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grows to maturity without any increase in cell number. This means that the cells of the outer epidermal layer keep pace in their elongation with the growth of the coleoptile. At maturity these very long thin cells attain in some instances a length of 3 mm., an increase of 150 times their embryonic "length".

The other layers (subepidermis, third layer, fourth layer and inner epidermis) show a considerable increase in the number of their constituent cells (in the long axis of the coleoptile), especially during the first quarter of the growth period. In segment *a* at the tip of the coleoptile, there is less

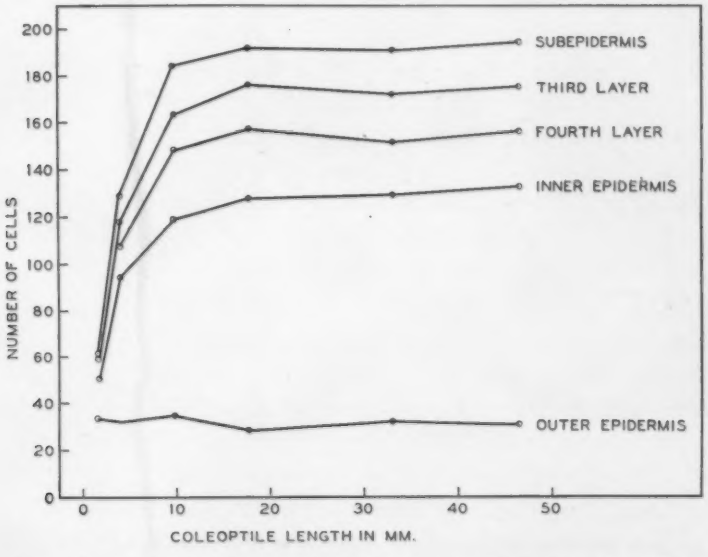

Fig. 5. Graph showing the number of cells from tip to base in the different layers of the *Avena* coleoptile, at six stages in its growth. Although the outer epidermal cells do not increase in number, the cells of the other layers multiply rapidly in the early period of development and then remain about constant in number. A definite gradient of cell-division intensity, decreasing inward from the subepidermis to the inner epidermis, is apparent for the first quarter of the growth period. During the last three quarters of its growth, elongation of the coleoptile is proportional to the elongation of all its constituent cells. Substantially similar results were obtained for *Triticum* (table 4).

cell division than in the other segments. The cells in the region above the tips of the vascular bundles, i.e., from the pore upward (figs. 3, 4), undergo neither elongation nor division.

When the total number of cells from tip to base in each layer is plotted against coleoptile length at each stage (fig. 5), the differential behavior of the various layers of parenchyma becomes evident. From the embryonic stage up to the time when the leaf bursts through the coleoptile, the

number of cells in the subepidermis increases 3.2 times, in the third layer 2.9 times, and the inner epidermis, 2.5 times; i.e., there is a distinct gradient from the subepidermis inward.

Embryo and mature coleoptiles were examined in transverse section at the base. There was no increase in the number of cells (fig. 6). Increase in cell number as well as cell elongation are taking place, only in the long axis of the organ, i.e., growth is distinctly *polarized*.

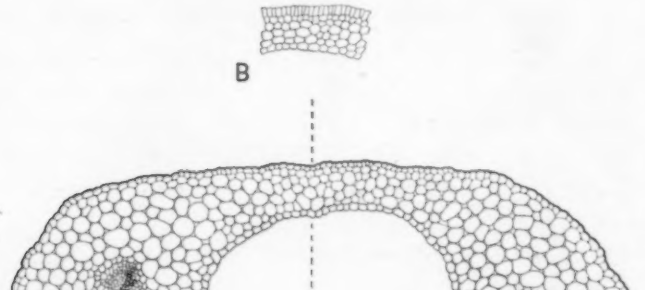

Fig. 6. A, transverse section of the lowermost end of a mature *Avena* coleoptile, ×40; B, transverse section of the narrow portion of the base of a 2 mm. long coleoptile. The number of cells is the same in transverse sections of young and old coleoptiles. The drawings for fig. 4 were made from sections cut in the plane indicated by the broken line.

DISCUSSION

Rothert (1894) first observed a shift in the zone of most rapid elongation in the growing coleoptile of *Avena*. He noted that maximum growth was taking place near the base in coleoptiles up to 12–15 mm. in length. In older plants growth had decreased at the base and the zone of most rapid elongation lay in the region about 10 mm. below the tip. These observations together with the results of more recent investigations on older coleoptiles (Went, 1928; Bonner, 1933), have led to the generally accepted conclusion that the lower zones grow more slowly than those nearer the tip. The experiments reported here, however, have shown that growth is

mainly basal during the period when the coleoptile is achieving the greater part of its length. In fact, it has been shown that the lower half of a 4 mm. coleoptile is responsible for nearly $\frac{3}{4}$ of the subsequent elongation. Relatively little growth in total length may be attributed to the region of maximum growth rate when it lies near the tip.

Söding (1929) investigated the distribution of growth hormone at different levels in *Avena* coleoptiles grown in the light; it was most abundant in the upper 1 mm., and decreased gradually downward until none could be demonstrated at the base. The tips of old coleoptiles, which have been broken through by the foliage leaf, contain little or no hormone.

In attempting to correlate hormone concentration with growth intensity, Thimann (1934) made extracts of successive segments from the apex downward in 26 mm. coleoptiles. Successively lower zones were successively less rich in the hormone. The tip 1 mm. segment was found to be 3.6×richer than the 1 mm. segment at the base. Hormone gradients have not been reported for coleoptiles in other stages of development. Laibach and Meyer (1935), however, found a high auxin content in seeds of *Zea*, the concentration falling off rapidly with germination. These facts suggest that auxin may be moving upward from the endosperm and cotyledon through the vascular bundles to the tip of the coleoptile from which point it is dispersed downward. Gradual depletion of the auxin supply might explain the decrease in growth rate and the acropetal migration of the maximum growth zone as the coleoptile nears maturity.

Bonner (1933) placed segments taken from the tips and bases of coleoptiles in solutions of the growth hormone. Segments from the upper third of the coleoptile showed a growth response more than twice as great as that of the lower segments. If these coleoptiles were 25–30 mm. long or longer (length not given), their degree of maturity at different levels as shown here, would explain the differential growth vigor of the isolated segments. It is probable that mature tissues near the base are incapable of growth when the food supply is exhausted (Went, 1935), even in the presence of favorable concentrations of the hormone. Furthermore, Went has shown that auxin becomes a limiting factor in the later stages of coleoptile growth. By the addition of more auxin, the ability to utilize the stored food in polarized growth is continued for a longer time.

The use of the *Avena* coleoptile as a quantitative test object for auxin has been based on the assumption that the hormone brings about increase in length only by cell elongation. It has been shown here that cell division takes place in the early stages of coleoptile growth, but this cell division ceases relatively early so that by the time the coleoptile is used for auxin tests, its elongation is directly proportional to the growth in length of its

constituent cells. Its use as a quantitative test object for hormones causing cell stretching is, therefore, valid.

SUMMARY

Determinations of relative growth rates on coleoptiles of *Avena* show the following:

1. The lower half of the embryonic coleoptile elongates to make up approximately three-fourths of the total length of the mature coleoptile. The upper half of the embryonic coleoptile elongates to make up the upper one-fourth of the mature coleoptile.

2. Although growth is taking place rapidly throughout the length of the coleoptile while it is young, the region of greatest elongation is basal. As the coleoptile nears maturity, growth slows down throughout its length, ceases at its base, and becomes *relatively* greater near its apex. At the time the foliage leaf bursts through, all basal growth has ceased, but a localized elongation region still remains at the tip, and this may persist for as much as 2 or 3 days after the leaf bursts through the coleoptile.

Cell counts and measurements on longitudinal median sections of growing coleoptiles show the following:

1. The number of epidermal cells remains the same throughout the growth period, i.e., on the average, their elongation is directly proportional to that of the coleoptile as a whole. The length of some of these cells increases as much as 150 times.

2. While the outer epidermal cells are elongating, the underlying parenchyma and inner epidermal cells on the average increase their number 2.9 times. At maturity the greatest number of cells is in the subepidermis, and each successive layer inward has fewer cells. This means that there have been fewer cell divisions in each successive layer inward from the subepidermis.

3. Most of the increase in numbers of cells takes place by the time the coleoptile is 1 cm. long, or about one-fourth of its final length. In this period the coleoptile increases in length as much as 14.7 times, while the gain in number of cells is 172%, or 2.7 times. In the balance of the growing period, up to maturity, the coleoptile increases in length as much as 4.6 times, while cell number gains only 7%, or 1.07 times. This further slight increase in numbers of cells takes place before the coleoptile is 18 mm. long. There is neither cell division nor cell enlargement in the tip between the pore and the apex. The increase in cells takes place below the pore and is about evenly distributed throughout.

4. Transverse sections of embryonic and mature coleoptiles show no appreciable difference in diameter, nor is there any increase in the number

of cells. Cell elongation and the increase in cell number take place only in the long axis of the organ, i.e., growth is *polarized*.

5. From (3) it is reasonable to conclude that cell division is not involved in coleoptile growth at the time it is used for growth hormone tests (Went technique). Growth in the later stages is directly proportional to the stretching of cells.

6. There is a brief discussion of the probable relationship between changing growth intensity and auxin concentration in the coleoptile.

The data given for growing coleoptiles of *Triticum* are substantially the same as for *Avena*.

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Cell size and organ size in two violet species and their hybrid[1]

J. W. Marvin

(with plate 1 and seven text-figures)

INTRODUCTION

An attempt to analyze the morphogenesis of an organ in terms of a summation of the development of its parts presupposes a more complete knowledge than we possess. Of the many cell and organ relationships, that of cell size to organ size was early recognized as important.

In metaphytes the achievement of organ size is a two-fold process—namely, the result of the auxesis and the meresis of the cells of the *Anlagen* accompanied by differentiation and physiological specialization. It seems significant that, in differentiated and mature tissue, cell size becomes fixed within certain limits and is a relatively constant character, as was suggested by Sachs (1877). Amelung (1893) showed it to be true for organs of different sizes on the same plant individual and on closely related plant individuals.

A study of some of the organs of a violet species hybrid and its parents shows the hybrid organ to have a specific cell size different from that of either parent. And further, depending upon the organ studied, the size of the cells in the hybrid organ may or may not be intermediate between the sizes of the cells of each of the parent organs.

LITERATURE REVIEW

Sachs' (1877) conception that there is a relatively constant cell size for a species was confirmed by Amelung (1893), Sierp (1913), Sinnott (1930), and many others.

Amelung measured cells from comparable regions on mature organs of the same plant individual. He found that cell size was relatively constant and that differences in organ size were due to a difference in the number of cells. He measured epidermal and palisade parenchymal cells as well as wood cells and fruit parenchymal cells. He found that a small leaf of *Ficus macrocarpa* had epidermal cells which were nearly the same size as the epidermal cells of a leaf twice as large. Also, the palisade parenchymal cells from a small leaf of *Buxus sempervirens* were of essentially the same size as cells from a leaf three times as long and three times as broad. Measurements of pith cells from different sized stems of *Sambucus niger*

[1] This investigation was carried on at the Vermont Agricultural Experiment Station, and the results are published with the permission of the Director, Dean J. L. Hills.

gave slightly different results. In a comparison of a long stem having a large diameter with a short stem having a small diameter, the large stem had pith cells which were considerably larger than those in the small stem.

Amelung also measured cells from comparable regions of mature organs on different plant individuals belonging to different genera of the same family. He compared palisade parenchymal cells from the large leaved *Rheum officinale* with those from the small leaved *Polygonum cuspidatum*. The area of the large leaf (*R. officinale*) was approximately fifty times greater than that of the small leaf (*P. cuspidatum*). This comparison showed the large leaf to have cells which were approximately 20% greater than those of the small leaf. Other similar comparisons did not show such marked results.

Tenopyr (1918) found that leaves of different shapes on the same plant individual were composed of cells of the same or of nearly the same shape. The ratio between the length and the width of basal orbicular leaves of *Campanula rotundifolia* was 0.92:1; the constituent epidermal cells had a length to width ratio of 1.02:1. Linear leaves from the stem with a length to width ratio of 14.15:1 possessed epidermal cells with a length to width ratio of 1.07:1.

She compared cells from different shaped leaves which were taken from two species of plantain, *Plantago major* and *P. lanceolata*. The ratio of leaf length to leaf width in *P. major* was 1.6:1, and the ratio between the length and the width of the lower epidermal cells was 0.75:1. In the case of *P. lanceolata* the length to width ratio of the entire leaf was 9.2:1, while the epidermal cells had a length to width ratio of 0.85:1. Thus leaves of different shapes from closely related plant individuals were also found to be composed of cells of nearly the same shape.

And further, she found that the average cell size for an organ in the mature condition was relatively constant for a species. This size may vary considerably, however, depending upon the stage of development of the plant at the time the organ was produced.

Sinnott (1930) has shown recently in an investigation of the length to width ratio of cells from different tissues of an organ that the cells do not respond in the same way to elongation of the organ. In a comparison of large and small petioles of *Acer saccharum*, he found that an increase in petiole diameter was accompanied by an increase in the size of the pith cells, and that an increase in petiole length was accompanied by an increase in pith cell size and number. There was, however, no correlation between epidermal cell size and organ size.

Lutman (1934) working on meristematic and mature differentiated

tissue shows that the lack of certain inorganic elements may stimulate early senescence and have a marked effect on cell size. He grew Japanese millet, rape, buckwheat, and garden beets in sand cultures using nutrient solutions in which either nitrogen, phosphorus, magnesium, potassium, or calcium was lacking. In other cultures these elements were in turn supplied in excess. Lutman found that the meristematic, undifferentiated cells of the root tips in millet, rape, and buckwheat which were grown in cultures lacking either nitrogen, phosphorus, magnesium, potassium, or calcium were prematurely vacuolate, had a reduced amount of stored food, and small nuclei. Each of these conditions is a sign of early senescence. Cells of the leaf epidermis of the same plants grown in solutions which lacked several of the so-called essential elements were smaller than comparable cells from plants grown in a complete culture solution. Further, the small cell size was correlated with the small size of the plant organs from which the cells were taken. A superabundance of any element used gave nearly the same results as the complete nutrient solution.

Macfarlane (1892), in an extensive study of many hybrids and their parents, considering external and internal morphology, found the hybrid to be an intermediate expression. He compared size, number, and position of hairs, the amount of cuticular deposit, the leaf venation, and the amount of secondary thickening in the parents and their hybrids. Reichert (1919) worked on starch grains in many different plants. He found, in a comparison of starch grains from parents and hybrids, that, while the hybrid starch grains were often intermediate, in many cases, they favored one or the other parent. Paulesco (1900) studied the morphology and anatomy of various spontaneous species hybrids (*Sorbus aria*×*S. aucuparia*, *Cistus longifolius*×*C. populifolius*, *Viola arenaria*×*V. riviniana*, *Viola mirabilis*×*V. sylvatica*, etc.) and their parents. He found that in many cases the hybrid characters were an intermediate expression. In other cases "juxtaposition" of some of the characters of each parent occurred; in still others he finds the hybrid to resemble very closely one of the parents.

MATERIALS AND METHODS

The plants used in these studies were collected from stock grown as part of the extensive violet project of the Vermont Agricultural Experiment Station. The parent species are inbred and are uniform strains which have been grown in the greenhouse for several years. In 1929 plants of *Viola conspersa* were pollinated with plants of *Viola papilionacea* by Dr. A. Gershoy. Several vigorous, sterile hybrid plants were obtained as a result of this cross, and these have since been propagated by mechanical division.

Material for histological study was fixed in chrom-acetic acid. It was found necessary to use the butyl alcohol method to prevent undue hardening of the tissue in imbedding. The sections were stained with either iron alum-haematoxylin or Flemming's triple stain.

The cells studied were drawn with a camera lucida at a magnification of 725 diameters. The areas of these cells were determined by the use of a planimeter. The readings, in square millimeters, were then converted into square microns. For each tissue studied, over two hundred cells of each parent and of the hybrid were measured. The arbitrary selection and measurement of cells from the regions studied is open to criticism, since some of the areas measured may not have been median sections of cells but rather, near one of the faces. The measurements, therefore, do not necessarily represent precisely the so-called specific cell size; they are comparable, however, and therefore are considered significant in this study.

Some difficulty was encountered in selecting comparable regions of the cortex, because, at the apex, there is little internodal stretching and the spirally arranged nodes are very close together. Since it was necessary for the purpose of this study to select a region in which the cortical cells were still nearly isodiametric and at the same time had attained maximum width before there occurred an appreciable stretching involved in the internode elongation, the cells in the first internode of appreciable elongation, below the apex, and near a branch meristem, were selected. The epidermal cells were taken from the upper epidermis of freshly gathered mature leaves from the basal portion of the stem. Hand sections were obtained from between large veins as near the center of the leaf blade as possible. These sections were mounted in glycerin and the areas of the cells computed.

OBSERVATIONS AND DATA

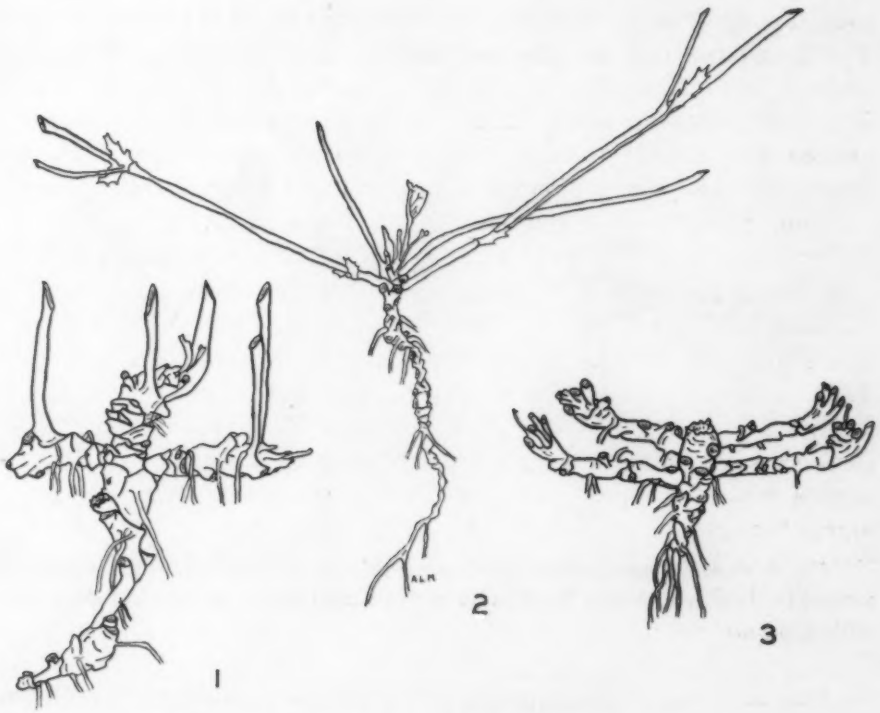
Stem and Leaves. A comparison of the visible characters of the species hybrid and its parents gives evidence that the morphological expression of the hybrid is intermediate, to a greater or lesser degree, depending upon the organ studied, between the morphological expression of each of the parents. Therefore, from a comprehensive study of the hybrid organism, it seems clear that one parent is no more potent than the other in expressing its morphological tendencies in the hybrid. From data presented here, there is no suggestion that the parents express themselves in the hybrid as a mosaic, but rather, it is evident that the hybrid is a compromise expression.

V. conspersa- Section Nominium Ging., Group Rosulantes Borb.:[1] this is

[1] A detailed discussion of the growth habits and affinities of the parent species is presented by Gershoy (1934).

a more or less erect blue violet with a slender, woody, indeterminate, orthotropic primary axis (see text fig. 2). Each year in the axils of the leaves are produced aerial leafy branches on which the flowers are borne; these branches usually die back to the base in the fall, although the basal portions may become persistent.

In the early summer and throughout the period of active growth, the cells of the cortex and pith of the determinate axis contain numerous



Figs. 1, 2, & 3. Diagrammatic sketches showing growth habits and relative sizes. Fig. 1. *Viola papilionacea*. Fig. 2. *V. conspersa*. Fig. 3. *V. conspersa* × *V. papilionacea*. Each figure 2/3 natural size.

plastids and store some starch. In the late summer and autumn these starch grains are hydrolyzed and possibly transported into the perennial stem. In section, the stretched and torn pith and cortical cells of the determinate axis show no starch. In the perennial axis, starch is found in the plastids of the cells of the pith and the cortex in the form of minute, compound grains.

The leaves borne on the aerial stem are comparatively small, and as a rule they are somewhat smaller than those shown in Plate 1, figs. 3a and

3b, which are formed earlier in the spring on the indeterminate axis. The characteristic form expression is that of an ovate blade with an acute apex. The margin is crenate and there is a moderately deep sinus. Blade size is variable depending upon the position (height) of the leaf on the shoot.

V. papilionacea- Section Nominium Ging., Group Boreali-Americanae Bckr.: the species of this group possess, characteristically, a fleshy, rhizomatous stem as a species character, and are perennials. The orthotropic axis (text fig. 1) in its stretching and elongation tends to become inclined. The lateral axes tend to curve and maintain a certain level at or beneath

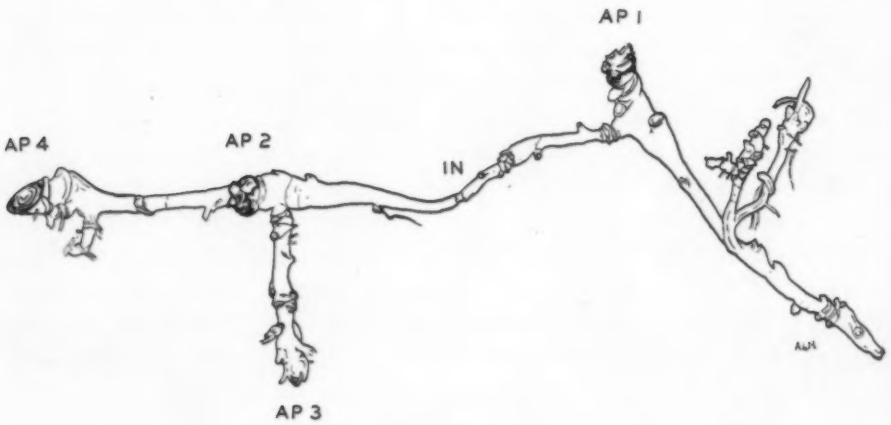


Fig. 4. A semi-diagrammatic sketch of the rhizome of *Viola papilionacea* illustrating the habit of growth and the relation of the lateral shoots to the main shoot. 2/5 natural size.

the surface of the soil. Undoubtedly, several factors control the curvatures. Text figure 4 illustrates the habit of growth and the relation of the lateral shoots to the main shoot. From below the terminal bud (*ap.* 1) of a primary axis arise one or more lateral, monopodial branches quite like the main axis. The growth of these branches is continued into the second season; at the end of the second season of growth, the terminal bud is usually not produced (*ap.* 2) and thus the growth of the perennial plant is continued by the lateral axes (*ap.* 3 and *ap.* 4). The proximal internodes (*in.*) may decay, thus setting free the individuals of a clone, as has been stated by Gershoy (1934). The individuals, aptly called "ramets" by Stout (1929), rapidly form swards in a suitable environment.

The leaves of *V. papilionacea* as compared with those of *V. conspersa* are relatively large. The blade, somewhat variable in shape and size, is

ovate-cordate with an acute apex, and at the base of the blade there is a deep sinus. (See Plate 1, figs. 1a and 1b, for leaf prints.)

Under favorable growth conditions, the hybrid, *V. conspersa*×*V. papilionacea*, produces a fleshy, orthotropic primary axis (text fig. 3). From this numerous lateral, rhizomatous shoots are produced; these plagiotropic axes extend on or near the surface of the soil. Morphologically, the hybrid stem is intermediate (text fig. 5). The internodes are appre-

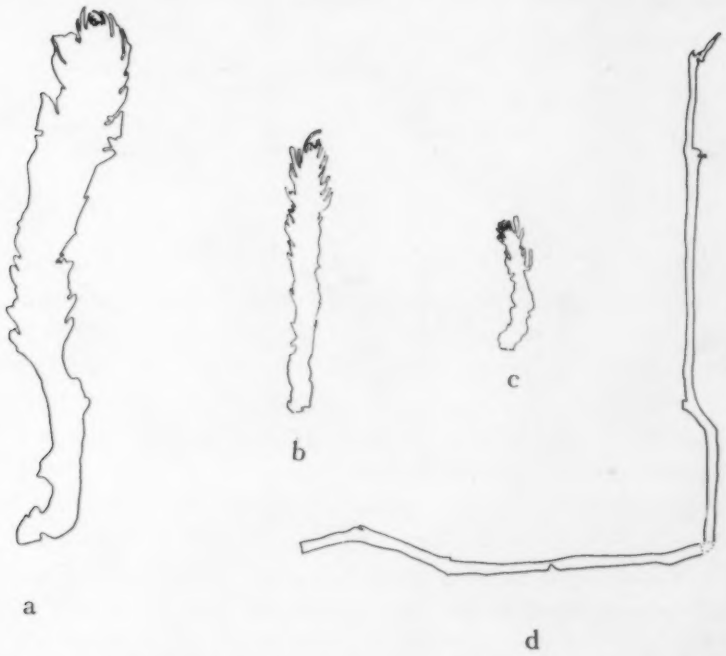


Fig. 5. This figure represents comparable figures, obtained from stained sections, of the stem axes of the two species and of the hybrid; *a* is a rhizome of *Viola papilionacea*, *b* is the rhizomatous axis of *V. conspersa*×*V. papilionacea*, and *c* & *d* are respectively the indeterminate and determinate axes of *V. conspersa*. Somewhat less than natural size.

ciably elongated. However, their length, although it approaches, does not equal that of the internodes of *V. papilionacea*. There are no aerial determinate axes such as are found in *V. conspersa;* the lateral axes of the hybrid are perennial or at least biennial.

Leaf size in the hybrid is variable. Usually, however, the hybrid leaves are larger than those of the seed parent and smaller than those of *V. papilionacea*. The hybrid leaf is also intermediate in character with regard to the depth of the sinus and the serration of the leaf margin. Plate 1

presents comparable figures, from the parents and the hybrid, of leaf form, size, venation, and the character of marginal serration.

CELL SIZE IN THE STEM AND THE LEAF

Cortical Cells in the Stem

The frequency polygons in text figure 6 show the distribution of the cortical cell sizes taken from longitudinal stem sections of *V. conspersa*,

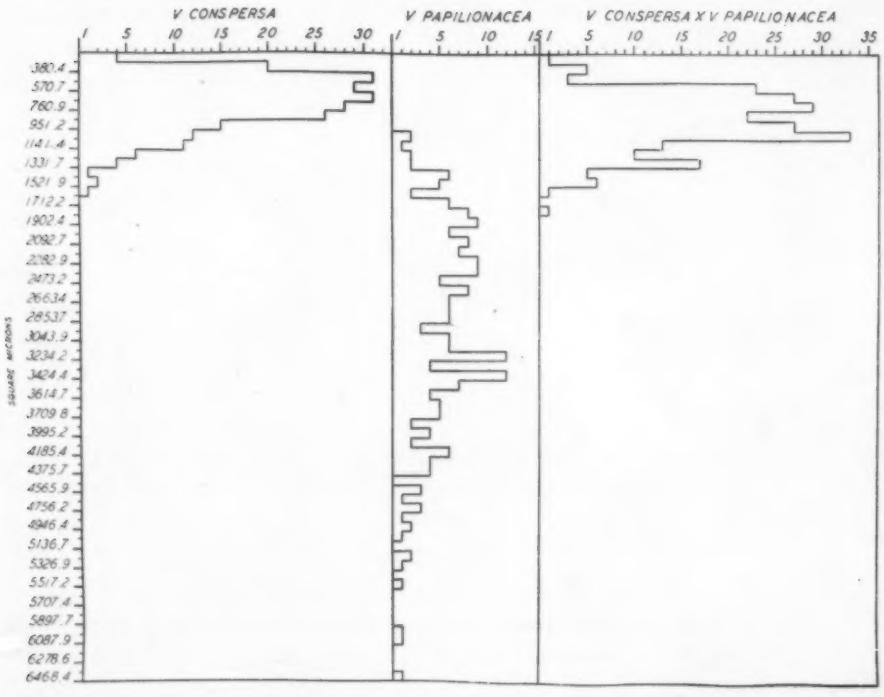


Fig. 6. Frequency polygons showing the distribution of the cortical cell sizes taken from longitudinal stem sections of *Viola conspersa*, *V. papilionacea*, and *V. conspersa* × *V. papilionacea*.

V. papilionacea, and the hybrid. The cells of *V. conspersa* show a narrow range of size, a definite modal class, and are the smallest in size. In *V. papilionacea* there is indicated a very wide range of cell size, a doubtful modal class, and the presence of much larger cells. In the hybrid the cell size is intermediate, the range in size distribution is narrow, and there is a definite modal class.

Since the cells of *V. papilionacea* show no well defined modal class, a weighted mean was computed for the curves. To obtain this weighted mean, the summation of the product of each frequency and its area was

divided by the total number of individuals. It is thought that this statistically determined weighted mean may be more indicative of a specific cell size characteristic of the tissue than is the modal class. Table 1 correlates roughly the size of the cortical cells with the size of the stem in the species and in the hybrid. In all three cases the cell size is represented by the computed weighted mean of two hundred cells in each case. Organ size is measured by the cross section area of the stem, and the relative sizes are presented as related to the largest size—namely, *V. papilionacea*, which is taken as 100.

TABLE 1

	CELL SIZE, SURFACE AREA (WEIGHTED MEAN) IN SQUARE MICRONS	ORGAN SIZE
V. conspersa	675.0	14
V. papilionacea	2784.0	100
Hybrid	873.0	40

There appears here, in a comparison of cortical cells from comparable organs of related species, a correlation between cell and organ size. The large organ has the larger cells, the small organ has the smaller cells, while in the hybrid, the size of the organ is intermediate, as is also the size of the cortical cells. Sinnott has shown that there is a correlation between cell and organ size in the pith cells of the petioles of *Acer saccharum*, and that in different petioles from the same tree, an increase in organ size is accompanied by an increase in cell size. Amelung, as noted, has shown that there is no correlation between cell and organ size for different leaves from the same plant individual, and for different genera in the same family—for example, he found that the palisade parenchymal cells in the large leaf of *Rheum officinale* were not at all proportionately larger than those from a related plant (*Polygonum cuspidatum*), though in a different genus, bearing small leaves. Cell size tends to be a constant, independent of organ size within the family limits. The size of the organ, according to Amelung, involves not primarily the size but the number of the cells. In the present case, for example, the cortical cells of *V. conspersa* are 24.2% as large as the cortical cells of *V. papilionacea*, whereas the organ is only 14% as large. In the hybrid the cells are 31.4% as large as they are in *V. papilionacea*, whereas the organ is 40% as large. The relative constancy of cell size and its independence of organ size is thus shown to hold true in hybridization.

Census growth, meresis, occurs in meristematic cells that are physiologically young—namely, cells with large nuclei, small vacuoles, and containing a large amount of stored food. Such cells are found in stem apices

and young root tips. Young (1933) has determined quantitatively the limits of the regions in corn root tips where cell division and cell elongation respectively predominate for the various tissues. The cells of the most specialized tissues early cease to divide and continue to grow by elongation only. In the cells of the pith, cell division accompanies elongation and this tissue shows individuality in this persistence of physiological youth. For each tissue, however, the specificity of its cell size in independence of the tissue mass is apparent.

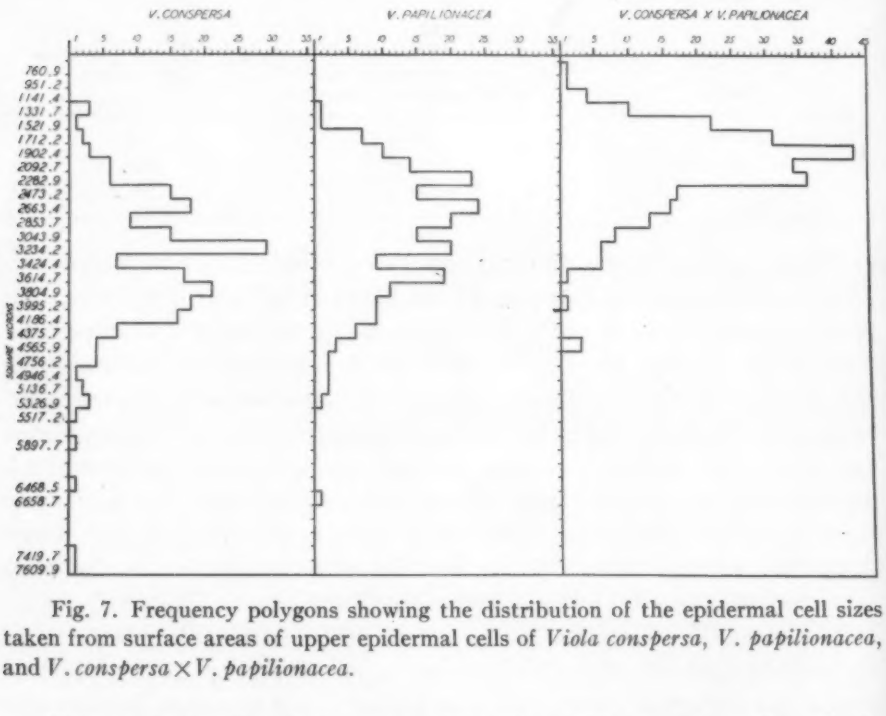


Fig. 7. Frequency polygons showing the distribution of the epidermal cell sizes taken from surface areas of upper epidermal cells of *Viola conspersa*, *V. papilionacea*, and *V. conspersa* × *V. papilionacea*.

The cortical cells of the perennial axis of *V. conspersa* show little anatomical differentiation. However, they early cease to divide and subsequently grow by elongation. This volume increase of the individual cells is quite independent of the shoot; it is primarily determined by the number of cell divisions (meresis).

The aerial determinate axes of *V. conspersa* show a marked elongation of the internode. The epidermal and cortical cells are elongated to several times their width parallel to the long axis of the organ. These cells contain large vacuoles and very little stored food. Mass growth, auxesis, continues so that some of the pith cells are actually torn. In this connection, Lutman's paper on senescence and rejuvenescence in the potato tuber

(1925) is of interest. He found that cells of the potato tuber were incapable of division when they lacked certain stored foods.

The production of the fleshy rhizome of *V. papilionacea* involves a well marked prolongation of cell division, which is accompanied also by a considerable range with respect to mass growth and the size of the cortical cells. These cells appear to contain a considerable amount of stored food, and they have small vacuoles. In a normal relationship between census growth and mass growth, the former precedes the latter. The demarcation between these two is in some cases very sharp as Young has shown. However, the cortical cells of *V. papilionacea* show considerable persistence in their physiological youth since both census and mass growth continue to occur rhythmically.

Epidermal Cells in the Leaf

The data obtained from measurements of epidermal cells are presented in text figure 7. The range in cell sizes in the two curves representing the two parent species is practically identical. Although there is no well defined modal class, in each curve the distributions are not the same. The curves do indicate, however, that *V. conspersa* has a greater average cell size than does *V. papilionacea*. In the hybrid the range is less extensive as compared with the parents; in addition, the hybrid has a smaller average cell size. In Table 2 a comparison of cell and organ size is made. In all three cases, the cell size for the two hundred cells measured is represented by the computed weighted mean. Organ size is represented in terms of relative blade areas; that of *V. papilionacea*, being the largest, is represented as 100.

TABLE 2

	CELL SIZE, SURFACE AREA (WEIGHTED MEAN) IN SQUARE MICRONS	ORGAN SIZE
V. conspersa	3242.6	16
V. papilionacea	3033.5	100
Hybrid	2070.8	45

It is apparent that *V. conspersa*, possessing the smallest leaves, has epidermal cells of the largest average size. The hybrid, with leaves of intermediate size, has cells of the smallest average size. *V. papilionacea*, producing the largest leaves, has cells that are intermediate in size. It seems evident here that, when parents and hybrid offspring are compared regarding cell size and organ size, there is no correlation between the size of the epidermal cells and the size of the leaf. Amelung found, in comparing organs of different size on the same plant individual, that differences in

organ size were not accompanied by differences in the size of the epidermal cells. Thus epidermal cell size was not correlated with organ size differences on the same individual. However, in his comparison of two genera with very widely different leaf sizes, *Rheum officinale* and *Polygonum cuspidatum*, he found in the cells of the palisade parenchyma a correlation between cell and organ size. This correlation was, however, by no means so marked as that between cell sizes from different sized organs but from the same individual.

Starch Grains

No attempt was made to plot the relative sizes of the starch grains. It appeared, however, from a careful examination of numerous cells, that the starch grains in the hybrid are intermediate in size between the small grains of *V. conspersa* and the large grains of *V. papilionacea*. In addition, it was observed that the grains of *V. conspersa* are several to many times compounded, while the grains of *V. papilionacea* are solitary, double, and rarely several times compounded. In the hybrid the degree of compounding seems to be intermediate.

DISCUSSION

The Leaf

It seems apparent, as shown in the photographs (Plate 1), that the size and form of the leaves in the hybrid manifests some degree of intermediate inheritance. From a study of the leaf prints, it seems clear that, in the shape of the leaf and in the character of the marginal serrations, the hybrid leaf is an intermediate, compromise expression. A study of the leaf blade areas of comparable leaves from the hybrid and its parents shows the hybrid organ to be intermediate in size. From these data, it appears that, in the size and shape of the leaf, the parents were equally potent in the degree to which their morphology was expressed in the hybrid.

The data from the measurements of epidermal cells as presented in text figure 7 show the distribution of cell sizes for the two parents to be nearly the same, with no well defined modal classes. The weighted means show the epidermal cells to be only slightly different in size although the organ size in one case is more than six times greater than the organ of the other parent. Tenopyr, however, has shown, in a comparison of the epidermal cells from the leaves of the common and the Witloof chicory, that there is a difference in the size of the epidermal cells, the leaves of the Witloof variety having larger cells than the leaves of the wild variety. Amelung and Sinnott have shown that epidermal cell size is not correlated with differences in organ size on the same individual. My data indicate

that the differences in size between the leaves of these two species is due to the number of cells rather than to the size of the cells, or to the combined effect of the size and the number of the cells. The hybrid leaf attains a size that is intermediate between the parent organs, and it is composed of cells considerably smaller than those found in the epidermis of the leaves of either parent.

The Stem

From the drawings of the stems of *V. conspersa*, *V. papilionacea*, and the hybrid, it seems apparent that the hybrid stem, while more thick and fleshy than the slender, woody stem of *V. conspersa*, is not equal in thickness to the stem of *V. papilionacea*. The perennial axes of the hybrid in which internode elongation has occurred have an internode length which approaches that found in the perennial axes of *V. papilionacea* and which is much longer than the internode length of *V. conspersa*. The thick, fleshy stem and lateral axes of the hybrid are strongly suggestive of the rhizomes of *V. papilionacea*. The perennial lateral axes are plagiotropic as are the lateral axes of *V. papilionacea;* the apices turn up, however, as if to become orthotropic. Some of the flowering aerial axes of *V. conspersa* may fail to attain their full growth in one season, and they persist into the following season. The internodes of such branches are short and the appearance of such partially condensed axes, oriented in a more or less transverse, geotropic position, resembles the elongated, rhizomatous axes of the hybrid. The axes of *V. papilionacea* contain much stored starch: the cells seem more densely crowded with starch grains than do the cells of *V. conspersa*.

For the material studied, the data indicate a representative cortical cell size for each parent and for the hybrid, that of the hybrid being intermediate between those of the parents. The works of Amelung, Sierp, Tenopyr, Sinnott, Lutman, and others show the difficulties which arise in an attempt to determine a specific cell size for a species. Thus the sizes determined as characteristic for the tissues studied here are not to be considered as specific cell sizes. However, for these data, it appears that, for comparable tissues from comparable regions, there is a representative cell size particular for the tissue, and this may be used in comparing cell and organ sizes.

According to the data presented herein, in comparing cortical cell sizes from stems of individual plants of related but not the same species, there is a correlation between cell and organ size. The large organ has cells which are larger than those of the small organ. This is in accord with Amelung's results where he compared palisade parenchymal cells from

comparable organs on two individuals of different genera but the same family. The hybrid organ is intermediate in size and the same is true for the size of its cortical cells.

From these data on the leaf and the stem, two observations are clear: 1) In both cases organ size is intermediate in the hybrid. 2) Cell size, however, may or may not be correlated with organ size when species are compared, depending upon the tissue studied.

That in some tissues of the hybrid the cells are intermediate in size, and that in others the cell size is smaller than in either or both of the parents is quite significant. The theoretical implications suggested are that the cell size is in part at least a function of the intercellular relations in an organ. These relations are influenced by the physiological-anatomical character of the organ, and in turn by the well known influence of functional factors on the intimate character of the cell. Environmental factors in their turn affect cell size. A discussion of these inter-relationships has been presented by Amelung (1893), and recently by Sinnott (1930), and Gershoy (1934). On the other hand, in organ size, in all cases studied, there is an intermediate expression of the parental characters. This expression seems to be influenced only secondarily by the functional and physiological factors affecting cell size, since cell size in these cases plays only a small part in the achievement of organ size. Organ size depends upon the number of cell divisions, a phenomenon which seems to be determined early in the ontogeny of the organ.

SUMMARY

A species hybrid, *Viola conspersa*×*V. papilionacea*, and its parents were compared in order to determine especially the cell size and organ size relationships in the leaf epidermis and the cortex of the stem.

1. In a comparison of epidermal cell size and organ size, there is no correlation, since, despite a wide range in organ size, epidermal cell size is relatively constant.

2. Cortical cell size and organ size were compared in the species hybrid and its parents. There is a correlation between cell and organ size: the largest cells are found in the larger organ.

3. From these data there seems to be a relatively constant cell size for the tissue studied. The hybrid cell size is different from that of either parent and, depending upon the tissue studied, may or may not be intermediate between the parental cell sizes.

4. In the two organs studied, the size of the hybrid organ is intermediate between the sizes of the parent organs.

5. From the frequency polygons of the epidermal and cortical cell

sizes, there is no suggestion that the range of cell size in the hybrid presents a mosaic pattern.

I am deeply indebted to Dr. A. Gershoy for the use of his material and for his stimulating criticism and advice. It is with considerable pleasure that I acknowledge the kind interest and many helpful suggestions of Professors R. A. Harper, G. P. Burns, and B. F. Lutman. The drawings, carefully prepared by Alice L. Marvin are gratefully acknowledged.

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Explanation of Plate 1

(all figures reduced to 4/5 natural size)

Fig. 1a. Mature basal leaf of *V. papilionacea*.

Fig. 1b. Mature leaf of *V. papilionacea*. This leaf was formed later than 1a.

Fig. 2a. Mature basal leaf of *V. conspersa* × *V. papilionacea*.

Fig. 2b. Mature leaf of *V. conspersa* × *V. papilionacea* formed later than 2a.

Fig. 3a. Mature basal leaf of *V. conspersa* borne on the indeterminate axis.

Fig. 3b. Mature leaf of *V. conspersa* borne on the indeterminate axis but formed later than 3a.

MARVIN: TWO VIOLET SPECIES

A new Houstonia in southcentral Texas

C. H. Mueller and Mary T. Mueller

During February and March, 1934[1] an apparently undescribed species of *Houstonia* was collected by the authors in various parts of Dewitt and Victoria Counties, Texas. It is found commonly scattered on the deep sandy prairie in open savannas of *Quercus marylandica* and *Q. stellata*.

The plant's annual habit and singly disposed flowers on erect peduncles which are never reflexed in fruit distinguish it from all other known species in our range except *H. minima* Beck., *H. parviflora* Holzinger, and *H. pusilla* Schoepf. [*H. minor* (Michx.) Britton]. From *H. minima* and *H. parviflora* it is distinguished by its corolla tube which much exceeds the calyx lobes. It differs from *H. pusilla* (with which it has frequently been confused) in having a light pink or lavender corolla yellow centered and hairy within the throat as well as more flat fruits and narrower leaves.

Houstonia pygmaea C. H. & M. T. Mueller sp. nov.

Annual; stems simple in young plants with the leaves forming a basal rosette, in older plants much branched at the base and subsequently forked, 1–2 cm. and finally 3 or 4 cm. long, procumbent or sometimes erect, forming a somewhat dense tuft except in shade forms which are slender; leaves finally distributed, the lower ones lanceolate to spathulate, the blades about 2×4–8 mm., acute, gradually tapering at the base into a petiole 2 or sometimes as much as 7 mm. long, the upper ones linear-lanceolate to broadly oblanceolate, short-petiolate or sessile, the blades about 1–2×4–6 mm., all blades and the wing-like edges of the petioles sparsely ciliate with short, thick hairs; stipules white, roughly ciliate, little more than a line between the leaf bases; peduncles erect, never horizontally disposed and never reflexed at maturity, slender, about 2.5–5 mm. long, accrescent; calyx lobes narrowly lanceolate, about 2 mm. long at flowering, sometimes becoming 3–4 mm. long and more broadly lanceolate in fruit; corolla infrequently persistent until the calyx lobes almost equal the tube, loosely salverform (hardly funnel-shaped), pink or lavender or sometimes almost white, the tube about 5 mm. long or a little less, much surpassing the calyx, the throat densely short, white hairy within, the limb about 6–9 mm. across, divided almost to the yellow throat into ovate, acute lobes 3–3.5 mm. (or rarely only 2 mm.) long and about 1.5–2.5 mm. broad; stamens inserted well above the middle of the corolla tube; style about 1 mm. long; stigmas narrowly oblong, densely short hairy, not spreading; fruit about two-thirds included in the hypanthium which reaches about 1.5 mm. in height, capsule didymous, very flat, about 2–2.5 mm. high, 3–4 mm. broad, and 1 mm. thick; seeds about 5–20 in each cell, minutely pitted and concave

[1] A very mild winter had permitted spring annuals to mature about a month early.

on the placental side, as large as 0.2×0.3×0.6 mm. when only five in a cell, but variously reduced in size when more numerous.

Annua, caules simplices vel ramosi, procumbentes vel erecti; folia ex lineari-lanceolatis late spathulata, inferiora petiolata, superiora sessilia, sparse ciliata, laminis 4–6 mm. longis 1–2 mm. latis; stipulae albae deciduae; pedunculi circiter 2–8 mm. longi erecti maturitate non reflexi; calycis lobi anguste lanceolati circiter 2 mm. longi accrescentes; corolla hypocrateriformis vel late infundibulariformis rosea vel pallide purpurea, tubo circiter 5 mm. longo calycem multo superante, limbo 6–9 m. lato centro flavo, fauce intus pubescente; fructus tertia parta ex hypanthio exsertus; capsula complanata 2–2.5 mm. alta, 3–4 mm. lata, 1 mm. crassa; semina in quoque loculo circiter 5–20.

Type specimens (Mueller nos. 3 and 4) collected February 16 and March 6, 1934 in Dewitt Co., Texas are deposited in the herbarium of the authors at Cuero, Texas. Co-types are preserved in the herbarium of the New York Botanical Garden.

CUERO, TEXAS

Additions to the genus Amsonia

ROBERT E. WOODSON, JR.

Since the appearance of the writer's monograph of *Amsonia* in 1928,[1] five additional species have been proposed from time to time extending both our knowledge of the biological entities of the genus and the synonymy concerned with pre-existing species. Shortly after the completion of the monograph, increased information regarding certain plants of the Ozark Plateau and adjacent territory to the southwest necessitated the recognition of *A. illustris* Woods.[2] as distinct from *A. Tabernaemontana* Walt. In 1931[3] two more species were reported from Arizona and Chihuahua respectively: *A. arizonica* A. Nels. and *A. filiformis* A. Nels. The former has subsequently been found to be conspecific with *A. pogonosepala* Woods., while the type collection of the latter (*C. G. Pringle 6796*) is likewise the type of *A. arenaria* Standl. More recently[4] two additional species have been reported from the Southwest, *A. grandiflora* Alexander and *A. lanata* Alexander, differing from *A. longiflora* Torr. and *A. tomentosa* Torr., respectively in little else than slight discrepancies in the dimensions of the corolla. It is obvious that in such ambiguous entities additional specimens augmented by field observation are greatly needed as aids to taxonomic interpretation. The same need is manifest with regard to the following "herbarium species" which appear to merit recognition:

Amsonia Peeblesii Woodson, spec. nov. Herbacea perennis plus minusve erecta 5–6 dm. alta; ramis ramulisque gracilibus glaberrimis; foliis alternatis rariusve approximatis linearielliptici apice obtuse acuminatis basi attenuatis 7–10 cm. longis 0.2–0.4 cm. latis superne minoribus glaberrimis subsessilibus; inflorescentiis irregulariter cymosis laxe plurivel paucifloris longiuscule pedunculatis (foliis valde superantibus); pedicellis 0.2–0.3 cm. longis post maturitatem paulo accrescentibus glabris; bracteis inconspicuis angustatis 0.1–0.2 cm. longis subfoliaceis; calycis laciniis linearibus obtuse acuminatus 0.6–0.65 cm. longis 0.05–0.07 cm. latis glabris vel apicem versus sparse pilosulo-barbellatis subfoliaceis; corollae tubo 1.7–1.8 cm. longo basi ca. 0.1 cm. diametro metiente prope insertionem staminum paulo ampliato deinde paululo angustato faucibus ca. 0.2 cm. diametro metientibus pallide livideque caeruleo prope basem etiam saturate extus glabro intus villosulo lobis oblique elliptico-ovatis obtusis 1.0–1.2 cm. longis patulis pallidissime caeruleis fere albidis; antheris 0.2 cm. longis paulo supra medio corollae tubi insertis; ovariis ovoideis ca. 0.15 cm. longis glaberrimis; stigmate capitato-maniculato apice

[1] Woodson, R. E., Jr. 1928. Ann. Mo. Bot. Gard. **15**: 379–434.

[2] Woodson, R. E., Jr. 1929. Loc. cit. **16**: 407.

[3] Nelson, A. 1931. Amer. Journ. Bot. **18**: 432; 433.

[4] Alexander, E. J. 1934. Torreya **34**: 116; 117.

obtuse bilobato; folliculis immaturis 10–12 cm. longis haud articulatis glaberrimis; seminibus ignotis.

ARIZONA: near Leupp, Coconino Co., May 27, 1934, *T. H. Kearney and R. H. Peebles 9568* (Herb. Missouri Bot. Garden, TYPE).

Mr. Peebles has added the following note concerning the affinities of this plant: "This plant belongs to subgenus *Sphinctosiphon*, having the stigma surmounted by two distinct lobes, and pods not constricted. It seems nearest *A. Palmeri* Gray, but the corolla lobes are 12 mm. long; calyx lobes are glabrous (rarely a single hair on margin)." The corolla tube is also decidedly longer in *A. Peeblesii* than in *A. Palmeri*, and the insertion of the stamens is somewhat lower within the corolla tube of the former, with a correspondent difference in the general shape of the throat. The same species has recently been collected by Mrs. McKelvie in the vicinity of Cameron, some distance down the Little Colorado River from Leupp.

Amsonia glaberrima Woodson, spec. nov. Herbacea perennis plus minusve erecta 6–7 dm. alta; ramis ramulisque glaberrimis gracilibus; foliis oblongo-ellipticis acute acuminatis 5–7 cm. longis 1.5–2.4 cm. latis glaberrimis firme membranaceis supra paululo lucescentibus subtus opacis; petiolis 0.2–0.4 cm. longis; inflorescentiis irregulariter cymosis aggregatis pauci- vel plurifloris breviuscule pedunculatis (foliis haud superantibus); pedicellis 0.3–0.35 cm. longis post maturitatem paulo accrescentibus glabris; bracteis inconspicuis linearibus vix 0.1 cm. aequantibus; calycis laciniis ovato-trigonalibus acutis 0.15 cm. longis glaberrimis; corollae tubo 0.65–0.7 cm. longo basi ca. 0.1 cm. diametro metiente deinde gradatim ampliato faucibus ca. 0.2 cm. diametro metientibus delicate caeruleo prope basem paululo fuscente extus omnino glaberrimo intus prope insertionem staminum villosulo lobis oblique ovatis obtusis 0.6–0.7 cm. longis dilute caeruleis glabris patulis; antheris ca. 0.1 cm. longis prope corollae fauces insertis; ovariis ovoideis ca. 0.1 cm. longis glabris; stigmate capitato-maniculato haud manifeste apiculato; folliculis immaturis gracillimis falcatis haud articulatis glaberrimis; seminibus ignotis.

LOUISIANA: low prairies, Welsh, Jeff Davis Parish, May 17, 1915, *E. J. Palmer 7660* (Herb. Missouri Bot. Garden, TYPE).

This plant appears to combine certain aspects of both *A. Tabernaemontana* and *A. ciliata*. The corolla is totally glabrous without, as in the latter species, while the leaves assume the size and shape of the former, although somewhat smaller than those of any specimens of it which are available for my observation in the herbarium collections of the Missouri Botanical Garden.

MISSOURI BOTANICAL GARDEN
WASHINGTON UNIVERSITY (ST. LOUIS)

Overwintering of Synchytrium decipiens in New York

J. S. KARLING

One of the many puzzling problems in relation to *Synchytrium decipiens* Far. is the manner in which this chytrid hibernates through the winter. Unlike the majority of species of this genus, it never forms, as far as is known, thick-walled resting sporangia to carry it over unfavorable seasons, but only summer sori and evanescent zoosporangia, which quickly collapse and die when exposed to the air. Furthermore, its host, *Falcata comosa* (*Amphicarpaea monoica*) is an annual which dies and dries up with the onset of cold weather and frost and does not reappear again until fairly late in the following spring. Yet in spite of these handicaps *S. decipiens*, when once established in a community of wild peanuts, almost invariably reappears on the host seedlings in the spring from year to year. The author's attention was first directed to the persistence of this parasite in 1931 while collecting material for cytological study of nuclear division, and careful observations were immediately begun in Van Cortlandt Park in New York City to record the appearance of the fungus as well as its method of hibernation. The upper part of this park is quite wild, shady and swampy, and the soil is continually damp and mucky, affording thus an exceptional environment for a luxuriant growth of the hog peanut.

In the course of these observations it was noted that in late September and early October deep seated, dark and shiny sori were formed on the stem, and in view of the fact that these did not dehisce at once when mature like the earlier orange colored ones it was assumed that they were dormant sori which remained alive during the winter and served thus to infect the host seedlings in the following spring. On this assumption seeds of *Falcata comosa* were collected and sown in the greenhouses at Columbia University during November of 1931, and the seed beds were then covered with a mat of heavily infected, dead stems and leaves of the host plant. When the seeds began to germinate in approximately three weeks, the beds with their covering were wetted thoroughly every day. As the seedlings emerged they were thus forced to grow and push through the wet covering of decayed and infected peanut stems and leaves, and ample opportunity was thereby afforded for infection in case the chytrid zoosporangia were still viable. Additional supplies of infected dried stems were brought in from time to time, and the experiment was duplicated during the successive winter months of that year to allow for the possibility that the fall sporangia of *S. decipiens* might require alternate thawing and freezing as well as a rest period for successful infection. The results for the winter of 1931–32 were all negative, and in the following winter the experiment was

again replicated without positive results. Out-of-doors, however, infection occurred in abundance during the spring as the host seedlings emerged from the ground. In 1932 the hog peanut seedlings emerged from the ground on April 29, but no infection was visible until May 10, when the plants were approximately two and a half inches tall. In 1933 abundant infection was found on May 14, and in the following year it was not until May 20 that any infection could be observed. The winter of that year was unusually cold in New York City with temperatures as low as −14°F., and traces of snow remained on the ground until late in March. In 1935 the winter was considerably milder, with the result that germinating underground fruits were found in abundance on April 15. However, no infection was found until May 25, when some of the plants were as much as six inches in height. From these records it seems apparent that infection occurs in the young seedling stage, possibly as they are emerging from the seed coat and ground, but does not become evident until somewhat later as the sori and zoosporangia mature.

It thus seemed obvious that some other means of hibernation than in the dead stems occurred. Attention was therefore directed to the underground fruits which are produced so abundantly by the hog peanut and remain alive in a dormant condition during the winter. It was immediately observed that these peanuts became heavily infected with *S. decipiens*, which develops deep seated and dark colored sori. Apparently infection occurs very early while the fruits are aerial, since infected, elongating flower stalks have frequently been observed. *Falcata comosa* forms both casmogamous and cleistogamous flowers, with the result that two kinds of fruits or seeds are to be found. The former develop into aerial, elongated, many-seeded pods, while in the latter the flower stalk begins to elongate after fertilization and forms usually a single-seeded fruit which grows into the ground, where it lies dormant until the following season. These underground peanuts are thus the only portion of the host plant besides the aerial casmogamous fruits which remain alive during the winter. It is not uncommon to find the pods of the latter also heavily infected with deep seated sori in the fall, but in no instances so far have I observed the parasite penetrating to the seeds themselves. The possibility that *S. decipiens* may be seed-borne is thus rather remote.

The sori which develop on the underground peanuts are strikingly similar in appearance to those formed late in the summer and fall on the stems and pods, and are confined without exception, as far as my observations go, to the thin outer covering of the fruits. No infection of the cotyledons has yet been found. The occurrence of these sori on the dormant underground fruits suggested at once that this was the manner by which

S. decipiens was carried over the winter. Accordingly in November and December of 1933 a large number of infected underground fruits were collected and planted in the greenhouses. Germination occurred within fourteen days, and after twenty-eight days when the seedlings were approximately three inches high 8% were found to be infected. These remained somewhat stunted in growth, but served as sources of infection, so that in a few weeks most of the plants were parasitized. Concurrent with these experiments sporangia from infected fruits were brought into the laboratory and mounted in hanging drops to test their viability. Germination was exceptionally sparse, and in only two instances were motile zoospores formed, indicating that the percentage of viability, in my material at least, is very low. Similar germination tests with infected underground fruits were made during the winter of 1934, and within approximately six weeks 14% of the seedlings showed infection. In these experiments as well as those of the previous year a small amount of soil from the field was allowed to remain on the fruits at the time of planting, which of course did not preclude the possibility that the fungus might have hibernated and been carried over in the adhering soil. With this in mind the peanuts were thoroughly washed before planting in 1935 so that no foreign material except the sori remained on the surface. In this season infection was as high as 18%.

In view of these experimental results and observations extending over a period of several years, it is apparent that, in the vicinity of New York City at least, the late summer and early fall sori and sporangia of *S. decipiens* may remain dormant on the coats of the underground fruits during the winter, and infect the young seedlings in the following spring. In Japan, however, according to Kusano (1932),[1] *S. decipiens* hibernates in the dead and dried vines. Kusano reports that the dark colored, deep seated dormant sori are never developed on the lower and older, but only on the upper portions of the host plant in the fall. Such dormant sori when brought into the laboratory at various intervals during the winter and kept fairly moist dehisced and liberated zoosporangia, which underwent cleavage and formed motile cells in from two hours to several days. The viability of the zoosporangia through the winter was found to depend primarily on moisture relations. Although Kusano succeeded in germinating the zoosporangia, he made no greenhouse tests to determine whether or not seedling infection would occur during the winter.

It is thus obvious that my observations and results on *S. decipiens* in the vicinity of New York City differ in many respects from those of

[1] Kusano, S. 1932. Dormancy in the summer sorus of Synchytrium. Jour. Coll. Agric. Imp. Univ. Tokyo **11**: 427–439.

Kusano in Japan. In the first place, abundant deep seated sori have been found in late summer and early fall on the lower and older as well as the younger portions of the vines in addition to those on the underground fruits. In many instances such sori have been seen to extend almost to the point where the vines emerge from the ground. Such infection apparently occurs on wet and rainy days as the zoosporangia and zoospores are carried downwards. Secondly, the zoosporangia from undehisced sori on dead and dried vines collected out-of-doors at various intervals during the winter have not only failed to germinate in hanging drops in the laboratory but also to produce infection of emerging seedlings in the greenhouses over a period of several years. In these tests conditions were made as favorable as possible for successful infection, but without positive results. Kusano does not report the occurrence of sori on the underground fruits, but it is probable that they were overlooked as sources of infection in Japan. While *Falcata comosa* is an annual, we have, nevertheless, in these underground fruits host tissues which are comparable, as far as hibernation of a parasite is concerned, to the stems and leaves of perennials. The fact that they occur underground insures in most instances sufficient moisture to keep the fungus alive in case, as Kusano claims, moisture is the dominant factor in viability.

There are thus, according to Kusano's and my observations, two means of hibernation of *S. decipiens* in *Falcata comosa:* (1) by dormant sori and zoosporangia in the dead and dried vines, and (2) on the underground fruits. However, the possibility that occasional resting spores are formed and thus serve as means of hibernation must not be excluded. Although no such structures have yet been observed, our search may not have been sufficiently intensive, and it is not altogether improbable that they may occur occasionally.

COLUMBIA UNIVERSITY
NEW YORK CITY

INDEX TO AMERICAN BOTANICAL LITERATURE
1931–1935

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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